A CRITICAL ANALYSIS OF THE DISTRIBUTION OF BIRDS IN A TROPICAL AFRICAN AREA

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"The ecological study of distribution involves so many details that it can best be carried on within restricted areas, where a personal familiarity with conditions is essential." (Chapin, 1932, p. 263.)

(*With* 1 *Figure in the Text.*)

1. INTRODUCTION.

SINCE 1928 I have been living in Usambara and, so far as official routine has permitted, I have been studying the birds with special reference to their distribution and its determinants. Various environmental factors have been regarded by different workers as of prime significance in this connection; and in order to concentrate local studies on the lines most likely to be fruitful I reviewed (1933*a*) the potentially significant variables with an eye to the peculiar conditions met with in Tropical Africa. I have since prepared (1935*a*) a synecological study of the Usambara Mountains, with special attention to the conclusions reached in the preliminary discussion. I have also taken each bird form represented in the area and endeavoured to define its local range in terms of the habitats, vegetation types and climatic types designated in the synecological study. Each species' temperature tolerance, bearing in mind ecoclimatic modifications, has also been indicated. It is unlikely that this catalogue will be published, but data of the nature it provides are essential when the attempt comes to be made to define the ranges of African birds in terms of ecological, and not merely by geographical, extension. I propose to deposit copies of it at the Natural History Museum.

Thus I have accumulated a mass of ecological data bearing on the distribution of birds in a compact but highly variable and mountainous area. I cannot claim to have studied any one species exhaustively; and it may naturally be asked how in such a locality, with much extremely dense vegetation, satisfactory determination of the ranges of the various birds has been possible. Actually I have made repeated traverses of critical areas, and I have brought together a collection of about 2000 specimens, selectively and with the constant object of obtaining both positive and negative evidence of the occurrence of particular species. Part of the collection has been described with field-notes (Sclater and Moreau, 1932 and 1933). Birds have also often been identified by knowledge of their notes and songs. My own work has been supplemented and constantly checked in the field by my wife and by a skilled African collector, to both of whom I am under a great debt.

On the whole, I have come to regard our delimitation of ranges, even for birds of Evergreen Forest, with a good deal of confidence, which certain incidents have strengthened. For example, after coming to the conclusion that *Oriolus chlorocephalus* and *Ploceus bicolor kersteni* did not range above about 4000 ft. I found published records of Usambara specimens from localities 1500 ft. higher (Friedmann, 1928). At my request Mr Arthur Loveridge kindly examined the actual specimens, which he had himself collected, and found that the data on the labels had been wrongly transcribed.

The present paper will be better appreciated if the synecological study with its maps and transect figure, published in the *Journal of Ecology* (1935*a*), is read first. The mountains consist mainly of two plateaux, 3000 and 4000 ft. high, bearing ridges up to 7500 ft. and surrounded by scarps. On biotic grounds I have defined three life-zones (1935): *Lowland*, up to 2500 ft.; *Intermediate* from 2500 to 4500 ft.; *Highland* from 4500 ft. upwards. The recognition of these three zones was forced on me as a result of personal field-work: preconception or suggestions from work elsewhere had no part whatever in forming my conclusions.

Evergreen Forest, of homogeneous facies, is present at all elevations in Humid and Semi-humid climates. In open country, on the other hand, the nature of the ground cover varies to an important extent. It tends to be harsh, tall and of vertical habit in the Lowland; dense, matted and recumbent in the Intermediate; a short turf in the Highland: while in contrast to all these permanent growths, in the Semi-arid section of the Lowland it is both scanty and ephemeral.

As regards climate, treated as a resultant of both temperature and rainfall, only Humid and Semi-humid occur on the plateaux. But in the surrounding Lowlands the climate ranges from Humid and Semi-humid on the seaward side, to Semi-arid in the rain-shadow under the western edge of the mountains.

We have records of 372 different species of (African) birds that we know, or believe, to be resident in Usambara, in an area of about 4000 square miles. Two species are each represented by two subspecies, and three others are each considered to be present in two forms, not at present recognised taxonomically, which may be called physiological races. This gives a total of 377 forms in Usambara, of which thirty-six are "water-birds". Some of the others are too imperfectly known to be used in this analysis, particularly certain Falconidae, Owls and Swifts, the study of whose residential distribution presents special difficulties. We are left with 294 "land birds" for which the ecological ranges can be presented with some confidence: and one might expect that, given this number of species and the peculiar nature of the area, some interesting principles bearing on the distribution of birds would emerge on analysis. I hope at least that this study may be in some measure what was in the mind of the great ornithologist whose words are quoted at the head of this paper. The fact that an entire fauna is subjected to analysis, and not merely certain elements

of it, will tend to minimise the risk of the selection of data, whether conscious or unconscious.

2. A SUMMARY OF FIELD OBSERVATIONS.

It is a truism that while no species is present in all situations at any given altitude, in a mountainous area most species also observe upper and lower limits of altitude. It will be convenient to consider their horizontal and their vertical ranges separately.

Horizontal range.

The outstanding feature of this is the profound dichotomy between the species inhabiting Evergreen Forest and other formations. Out of all the 294 birds we have under consideration only about a score are encountered both in Forest and outside it. Moreover, most of these are birds (like *Camaroptera brevicaudata griseigula* and *Tympanistria t. fraseri*) that frequent the edges of Evergreen Forest without penetrating its depths, and whose habitat elsewhere is dense, and often tall, semi-deciduous bush. The birds that can be said to be in any sense at home both in a climax community of Forest and in another natural formation are limited to six, viz.:

(*a*) *Lophoceros melanoleucos* (a Hornbill), *Dendropicos lafresnayi hartlaubii* (a Woodpecker), *Campephaga flava* (a Cuckoo-shrike);

(*b*) *Psalidoprocne holomelaena massaica* (a Bank Martin);

(*c*) *Tchitrea viridis suahelica*, a Paradise Flycatcher exhibiting different colour phases inside and outside Forest, which may have to be recognised taxonomically (Sclater and Moreau, 1933, p. 8);

(*d*) *Apalis flavida* (*golzi*), a "Bush-Warbler" similarly represented by two forms, included under the same name but perhaps actually good species.

Only (*a*) and (*b*) can count as wholly undifferentiated forms, and the habitat of the Martin is not primarily conditioned by vegetation. There remain the three birds in (*a*), which all live high in the trees and appear to be Savannah species exhibiting unusual adaptability. The dichotomy between the Forest and extra-Forest faunas is thus practically complete. Bates (1931) demonstrated a similar state of affairs in West Africa, so that in all probability it holds good for Africa generally. To some extent the cleavage goes even deeper than the species. Among the genera (of "land-birds") occurring in Usambara there are seventy-four that each provide more than one (and up to six) species. But only twenty-three of the seventy-four genera are represented both in Forest and in other formations, by different species.

The clearings that have been made in the primary forest afford some means of gauging the relative degrees of adaptability of the two faunas. As a consequence of clearing, a variety of strange habitats is exposed in immediate proximity to forest birds. The habitats conditioned by cultivation range from well-tilled or closely grazed land, through coffee plantations with ample bush-growth and shade-trees, to fairly dense and tall plantations of exotic trees.

Clearings not in active use show every stage of regenerating forest. The Evergreen Forest fauna of Usambara numbers eighty-eight species, including those characteristic of the edges. Practically only one of them, the little Fly-catcher, *Alseonax minimus roehli*, has adapted itself to life in areas under any form of cultivation. In land lying fallow and where forest regeneration is proceeding unchecked, no member of the Forest fauna takes up residence until the Bush stage has been succeeded by the Small Tree stage, and something like a recognisable canopy has been formed. A few pioneers of the Forest fauna then occupy the growing Secondary, but they are as a rule species that in the Climax Forest belong to its edges.

About one-third of the eighty-eight Forest species make what can best be described as foraging raids into clearings and among introduced plants. Nearly all these comparatively enterprising species belong to the canopy of the Forest, and among them insectivorous birds are much in the minority. Most are fruit-eaters. Some of the remaining sixty species of the Forest fauna have occasionally been seen to make a hurried direct flight across a clearing, but in general they confine their excursions to within a few feet of the Forest edge.

The clearing of Forest thus involves an almost total disappearance of its fauna, which fails to occupy land under crop or secondary growth until the latter has reached an advanced stage. This is the more noteworthy because the Forest fauna is presumably under a kind of economic pressure to utilise the clearing habitats. The Forest has been constantly reduced, in some localities rapidly and to a mere vestige of the area it occupied 50 years ago, so that a crowding effect within its bounds seems inevitable. Meanwhile the cleared areas are populated in the main by immigrants from the Savannah, though at high altitudes a small special fauna is in possession.

Although so closely restricting themselves to the Forest formation, within its limits individual species of Forest birds are found to inhabit communities of highly dissimilar aspect and specific composition. Thus, in the Highland Zone the Forest formation occurs in both Humid and Semi-humid climates: in the former it is represented by a Broad-leaf community and by Mountain Bush (which often looks like Small Tree secondary growth); in the Semi-humid by "Cedar" Forest (*Juniperus*) with needle foliage and a comparatively light and sparse growth. The Highland Broad-leaf community resembles the Intermediate and Lowland Forests much more in general aspect than it does the Mountain Bush or the Cedar. Yet most of the Highland Forest fauna is common to all three of the dissimilar Highland communities.[1]

In forms that occur in more than one altitudinal zone, adherence throughout to the same type of habitat is the rule. Thus, a bird belonging in the Lowland to the Forest ground-stratum habitat, with an equable eco-climate

[1] Elton (1935) has recently shown that in England "there is not much difference between the bird communities of deciduous and conifer woods", a case parallel to that of the Highland Broad-leaf and "Cedar" communities in the West Usambaras.

characterised by low maxima, does not at higher levels tend to emerge into more open situations where the higher eco-climatic maxima can compensate for the lowering of the standard maxima by the increase in altitude.

The differences between the Forest and the Parkland formations are clear-cut. For this reason attention has been focused upon them both here and in the preliminary synecological study. But Parkland embraces a range of communities with at one extreme the Semi-arid *Acacia-Sansevieria* Thorn-bush with ephemeral ground cover, and at the other the Long-grass Short-tree Savannah of the Semi-humid. The Thorn-bush, although classified in the same botanical formation, shares only about one-fifth of its bird-fauna with the Semi-humid Savannah. This proportion is maintained in the Tree Habitats of the two communities, where the environmental differences are less glaringly obvious than in the Ground Habitats, although the specific difference in the vegetation is still high.

Where a swampy river valley (the Mkomasi) traverses the Semi-arid it supports a strip of native cultivation, of permanent grassland that is grazed by cattle, with a few trees and bushes, and of typical swamp vegetation, all surrounded by Thorn-bush of an extreme type. Thus to some extent "control" conditions are provided; for although in the river valley itself the influence of the swamp tends to modify the Semi-arid standard climate the high winds prevalent in the area minimise this eco-climatic effect. We have in fact in the Semi-arid climatic type vegetation of the kind that occurs also in the Semi-humid (as well as in the Humid). It is, then, interesting to find that none of the birds inhabiting the riverain strip of the Mkomasi Valley belong to the surrounding Thorn-bush, and with two exceptions they are forms also found in the wetter climatic types in Usambara. A particularly interesting instance is that of the Black-headed Weavers. A colony nesting in a tree in the cultivation proved to be not *Ploceus intermedius*, the species resident in the Thorn-bush a short distance away, but *P. nigriceps*, a bird of practically identical feeding and nesting habits, typically occurring in Savannah and cultivation in the Semi-humid and Humid. In fact, faunal composition there follows floral composition irrespective of climatic type.

Vertical range.

It will make for clarity if we deal with the Forest fauna separately from the other; because the Evergreen Forest formation is peculiar in presenting an approximately homogeneous facies from sea-level to 7500 ft. Of the eighty-eight Forest forms only eleven appear to exist in any number throughout the three zones. They have nothing else in common, for they include a Francolin, a Cuckoo, two Barbets, two Honey-guides, two Flycatchers, a Cuckoo Shrike, a Drongo and a Starling.[1] There remain seventy-seven forms showing vertical

[1] *Francolinus squamatus usambarae, Chrysococcyx cupreus intermedius, Viridibucco simplex, Buccanodon leucotis kilimense, Indicator variegatus, Prodotiscus insignis ellenbecki, Tchitrea viridis suahelicus, Batis mixta, Coracina caesia pura, Dicrurus l. ludwigii, Onychognathus w. walleri.*

restriction. Of these twenty-seven are confined to a single zone, sixteen of them to the Lowland, two to the Intermediate and nine to the Highland. Fifty belong to two zones only, made up of twenty-one inhabiting both Lowland and Intermediate, and twenty-nine common to Intermediate and Highland. Thus, with practically a third of all the forms restricted to a single zone, and half of them to two, zonation, even in the homogeneous Forest formation, is a very real thing. Moreover it takes effect at quite low altitudes, within 3000 ft. of sea-level.

It is surprising to find that comparatively few genera are represented by different species in the Highland and the Lowland Zone respectively. The Forest fauna includes sixty-seven genera, only thirteen of which have more than one species in Usambara; and of these thirteen, four are Highland (and Intermediate) and two others (*Alethe* and *Apalis*) are almost certainly in reality heterogeneous. Thus the phylogenetic relationship between the Lowland Forest fauna and the Highland Forest fauna can only be called remote. Chapin (1932) finds the same situation in West Africa.

In general the boundaries to vertical range are astonishingly abrupt. A few species characteristic of the Intermediate and Highland Forests make sporadic appearances in the Lowland, but for the most part the transition from abundance to absence appears to be sudden, taking place within 500 ft. of altitude. This is well marked on the East Usambara plateau, where the Highland elements of the Intermediate fauna are in full force at 2800 ft., but over the edge of the scarp, at 2000 ft., may be sought in vain, even where the mantle of forest is unbroken (see Map 2 in Moreau, 1935*a*).

In the non-forest fauna, amounting to about 200 species, a much larger proportion is confined to a single zone than among the Forest fauna. Indeed, the majority of them make no appearance above the Lowland Zone. The difference between the two faunas in this respect is probably in great measure, if not wholly, due to two facts: unlike the Forest, the non-forest is vastly greater in extent in the Lowland than in the other zones; and the non-forest embraces several different climatic and vegetational types no one of which finds a close counterpart at higher altitudes, except that the small area of Tall Grassland in the Intermediate shows a general resemblance to one kind of Savannah.

The non-forest fauna of about 200 species includes only sixteen that do not occur in the Lowland. Of these, seven are exclusively Highland birds, while the other nine are shared with the Intermediate. Ten species,[1] again with nothing in common, range through all three zones, though most of them give the impression of being least common in the Highland.

[1] *Streptopelia semitorquata* (Dove), *Cuculus solitarius*, *Lampromorpha klaasi* (Parasitic Cuckoos), *Centropus superciliosus loandae* (Coucal), *Colius striatus affinis* (Coly), *Anthus richardi lacuum* (Pipit), *Dryoscopus cubla hamatus* (Shrike), *Buphagus erythorhynchus caffer* (Oxpecker), *Spermestes n. nigriceps* and *Estrilda astrild minor* (small Weavers).

Whether Forest or non-forest birds are considered, there appears to be practically no seasonal movement up and down the mountains. Van Someren has kindly informed me *in litt.* that the same applies to the Kenya Highlands. The only definite exception in Usambara is a Swallow, *Hirundo abyssinica unitatis*, which during the four coldest months of the year leaves the plateaux, which are within its breeding range, for the Lowland Zone. (Several other species of hirundines and swifts are sedentary on the plateaux all the year round.) The remarkable rigidity of most species' altitude limits is particularly exemplified by two long-tailed Sunbirds, *Nectarinia famosa aenigularis* and *Drepanorhynchus reichenowi*, constantly encountered from 5000 ft. upwards. Their favourite food-plant, a *Leonotis*, is not similarly limited. I am well acquainted with one slope extending from 4000 ft. up to 5500 ft. on which *Leonotis* occurs throughout; but the two species of Sunbird are not encountered on it below 5000 ft. at any season. Again, as I have mentioned elsewhere, several species of Forest birds confined to over 4000 ft. in the West Usambara plateau also occur on the detached Eastern block only on the one ridge surpassing that height.

The definite nature of the zonation is emphasised rather than obscured by the attempts that some birds appear to make to transcend its limits, nearly always unsuccessfully. Thus, in the last six years several Lowland species have made appearances, some of them more than transitory, in the Amani clearing, which is just within the Intermediate Zone (3000 ft.). Several conspicuous instances can be quoted where the normal absence of the birds in question cannot be considered obligate, nor, since the clearings have existed for thirty years, can it be attributed to time-lag. The magnificent *Euplectes hordeacea changamwensis* may appear for a day or two and vanish again. In the nearby Lowland an occasional nesting site of these Bishops is in *Panicum maximum*; but they do not ascend the mountain sides as high as the grass does. Wagtails (*Motacilla aguimp vidua*) have occurred in two clearings in the Intermediate more or less continuously since 1930. They often sing vigorously from buildings as they do in the Lowland, more than once pairs have been present and nests have been built, but the birds never seem to have bred or even laid eggs. *Malaconotus poliocephalus*, the Giant Shrike, which utilises exotic trees in the Lowland, was common and noisy in the Amani plantations in 1929 and has hardly been heard there since. The one successful colonist from lower levels during the period under review is *Actophilus africanus*, the Lily-trotter, which appeared on a millpond in the Intermediate Zone in 1930 and has brought off several broods.

A few species appear to have a curiously discontinuous vertical distribution. *Oena capensis* (Dove), *Sigmodus retzii graculinus* (Shrike), *Eurystomus afer suahelicus* (Roller), *Uraeginthus bengalus ugogoensis* (Weaver), all common in the Lowland, have been observed in the Highland Semi-humid, although nowhere in the Intermediate. Again, the Drongo, *Dicrurus adsimilis divaricatus*,

common in the Lowland Savannah and in an Intermediate Humid clearing at 3000 ft., misses the Intermediate Semi-humid and only reappears in the Highland Semi-humid. But the status of these species in the Highland is not quite certain. For all of them the vegetation where they occur in the Highland is unlike, both in species and in appearance, that of their normal associations in the Lowland.

An interesting feature is exhibited by certain species—e.g. *Apaloderma narina* (a Trogon), *Trococercus bivittatus* (a Flycatcher) and, outside the Forest, *Eremomela scotops* (a Warbler) and *Oriolus monacha*—represented in Kenya by one race in the narrow Semi-humid coastal strip and by a second in the highlands. There each conspecific pair of races is separated by a wide belt of Semi-arid country from which the species is absent. Since there is no land surface in the coastal strip higher than about 1200 ft. above the sea, that is the obligate altitudinal limit of the coastal races. In Usambara, where the birds of these species are identifiable morphologically with the Kenya coastal forms, there exists no limitation, either vegetational or geographical, to the extension of their range up into the same altitude as is inhabited by their congeners of the Kenya Highlands. Yet in Usambara these coastal races are confined to the Lowland Zone; and the species to which they belong have no representatives in the Intermediate or Highland.

Where Usambara species occur in an identical form in other mountainous areas also close to the Equator, their altitudinal limits may usefully be compared. I am able to draw on personal observations for Kilimanjaro, on Ogilvie-Grant (1910) for Ruwenzori, and on Van Someren (1922 and 1932) for the Kenya Highlands. Of twenty-one forms belonging to the Highland and Intermediate in Usambara sixteen have their lower limits at lower altitudes on Usambara than on the other mountains named, four are the same, and one, *Pseudoalcippe abyssinicus*, apparently higher (about 1000 ft., compared with Kilimanjaro). Of eight species confined to Lowland plus Intermediate in Usambara, all reach higher altitudes elsewhere. Thus there is a general indication that the limits of the avifaunal zones are drawn at lower altitudes in Usambara than elsewhere in the same latitudes. Unfortunately we have no good temperature data for Ruwenzori or Kilimanjaro, but the indications are that, like the Kenya Highlands, they are warmer than Usambara at the same levels (Moreau, 1934). The question is, however, complicated by the amount of clearing that has been done on the other mountain-masses, which has resulted in an artificial restriction of Forest.

3. Distribution and the significant variables.

In a recent preliminary review (1934) I considered the significant variables under the heads of Biotic, Climatic and Subjective Factors. It will be convenient to follow this general division, but to refer only to those particular factors considered likely to be of general significance.

(*a*) *Biotic factors.*

I used this term to cover "the most obvious and concrete elements in a species' economy; the presence or absence of suitable food, nesting-sites, nesting-material, of enemies and of competitive species". As I pointed out, "suitable" is the universal, but question-begging, epithet in this connection. For the present we will consider the presence of suitable food, etc., *in type*. Thus, the existence of fish of manageable size for a fish-eater, of fibres for a bird whose nest is always made of a variety of fibres, of vertical grass-stems for a bird whose nest architecture depends on such supports, may be regarded as Biotic Factors in type. Such prime requirements are decisive in determining range. In an area where they are lacking a bird's absence may be said to be obligate, where they are present and the bird is not, its absence is facultative—to borrow a convenient pair of terms from parasitology.

Judged on these lines, what proportion of birds can be said to show an obligate limitation to their observed ranges? For how many forms of insect-feeders, or for the builders of cup-nests of fibres among bushy growth, or for the birds that search bark for insects, can their distribution be said to cover in any one locality all the habitats where these prime essentials are available in type? Very few. In Usambara the observed limitations of range can be said to be obligate mainly in two categories:

(*a*) "Water-birds", which are mostly common only in the Lowland Zone. Above that, water exists mainly in mountain torrents with few or no fish.

(*b*) Birds building in tall grass of vertical habit. In the Intermediate and Highland Zones the habit of the grasses is neither robust nor vertical.

A few other instances of obligate absence can be cited: big Hornbills (*Bycanistes cristatus*) from the Savannah where trees with big enough nesting-holes are lacking; Palm-swifts (*Tachynautes parvus myochrous*) from the Highland Zone where there are no Palms nor Dracaenas with strong mid-ribs for them to gum their nests on; *Spermophaga ruficapilla cana*, the heavy-billed Forest Weaver, from the Highland, where the only large-seeded forest grass, *Olyra latifolia*, its staple food, is absent; Vultures from the Highland and Intermediate, where no quantity of carrion is available. On first appearance the absence of the Golden and Black-headed Weavers (*Ploceus aureoflavus* and *P. nigriceps*) from the Intermediate Zone of the East Usambaras might also be put down as obligate, since the tropical grasses on which they are often found feeding in the Lowland Zone, at the bottom of the "Sigi Hill" (see Map 2 in Moreau, 1935), fade out before the top of the hill is reached. But in fact these two Weavers' local restriction can hardly be obligate because *P. aureoflavus* is established in the Intermediate Semi-humid of the West Usambaras, where the tropical grasses are totally lacking. The broad generalisation remains, in hardly one-tenth of the whole fauna can it be said that the observed limits of distribution appear obligate.

The criticisms of the propriety of such a generalisation are obvious. It is of course true that we are dealing with an imperfectly known fauna, no single member of which has been studied exhaustively. But within the limits of my definition of Biotic Factors I doubt whether workers in the most intensively studied Temperate fauna would disagree with it. It can be objected that by using a definition drawn in such wide terms the conclusion is stultified. I do not agree. I hold rather that, while not failing to allow for our ignorance, we do by this means tend to throw into relief those factors in distribution that are subtle, discriminatory, or as I have called them, subjective.

To some extent this generalisation stands or falls by the view that is taken of the food requirements of birds. Is it a general rule, for example, that to a given insectivorous bird certain species, or it may be, genera, of insects are essential to life? The weight of opinion and experience is against it, though there are of course specific exceptions. The point would be settled outright if we could accept McAtee's conclusion (1932), based on a huge volume of data, that no discrimination between groups of prey takes place on the part of birds. But he seems to go too far and Cott's criticism (1932) is effective. McAtee's data do, however, show that a bird will take a wide variety of whatever is available in its habitat, and that discrimination is limited. Roberts (1934), in his Iceland ecological work, has stated a somewhat similar conclusion happily and judiciously. "An examination of the food-records...tends to show that a bird will eat whatever food it can obtain with the least difficulty in its own particular habitat. We did not find reason to think that any bird selected an area because a type of food which it ate existed there in greatest quantity." The data of neither of these authors come from the Tropics, where indeed little is known about bird food, but there is reason to accept the general applicability of their conclusions. They are in fact supported by the small amount of stomach examination done at this Research Station, and even by the data obtained (Moreau, 1933*b*) for the specialised Oxpecker which takes such insects, however diverse, as find themselves on the hide of a beast. Again, the stomach of a single Akalat or Nightjar contains representatives of half a dozen different orders of insects and other invertebrates;[1] a series of these birds includes an immense variety of prey. Yet the Akalat in question is confined to the interior of Forest below 4000 ft., there to be replaced by another species of similar habits. The Nightjar abounds on the roads and clearings in the Lowland but does not appear in clearings a few hundred feet farther up the mountain side except as a rarity, nor follow a road through a patch of forest, although in these unfrequented situations insects of many kinds are abroad at night. Again, a Pigeon (*Columba arquatrix*), that has been shown by Phillips (1927) to consume a great variety of dissimilar wild fruits, is common in the Highland Forests

[1] E.g. *Illadopsis rufipennis distans* no. 722; wood-lice, Elaterid larva, earwigs, centipedes, spiders, Hymenoptera. *Caprimulgus fossii mossambiquus* no. 1843; grasshoppers, moths, beetles (6 species), Pentatomid and other bugs, a froghopper, a Membracid

of Usambara, but almost unknown, even as a foraging visitant, in the Intermediate Humid with its much richer display of fruit-bearing trees.

I personally cannot believe that in such cases as these the birds' absence from the unfrequented environments is due to the impossibility of amassing a satisfactory miscellaneous collection of food.

A similar argument could be developed as regards nesting and nesting sites. Enemies, with so great a variety of predators in every formation and zone, cannot be regarded as competent to produce the observed general limitations, even if a degree of discrimination, that is unlikely, could be demonstrated in individual predators. The presence of the vectors of parasitic diseases at lower levels might conceivably limit the downward projection of Highland species; I know of no such factor that could be effective in producing an upper limit to the range of Lowland species.

I conclude that Biotic Factors in general, as I have defined them—the presence or absence of essential requirements—cannot account for any larger proportion of the observed limitations than the food factor discussed more freely above.

(*b*) *Birds and temperature.*

In my study (1935*a*) I have used the mean maxima of the three hottest months and the mean minima of the three coldest to delimit the temperature ranges of the local birds. If the means are taken for the single hottest and the single coldest month the maxima and minima are each exaggerated by about 1° C.

For convenience of reference the figure showing the temperature×altitude gradients in Usambara (Moreau, 1935*a*) is reproduced here in a simplified form (Fig. 1). The necessary explanation of its basis and arrangement is given in the paper quoted. It is unfortunate that no temperature data are available for any station at a lower altitude than 1500 ft., where the maxima are between 32 and 33° C., except Tanga, on the shore-line, with maxima of 31° C. Apart from the influence of the sea breezes the maxima might be expected to rise 1° C. for every 1000 ft. reduction in altitude. I have therefore adopted 34° C. as the mean of the standard maxima at the bottom of the Lowland Zone.

As a general rule, which holds good in Usambara, the standard minima fall off with increasing altitude more rapidly than the maxima, so that, eco-climatic modifications apart, the daily and the annual ranges are greater at high altitudes than at low ones: and of two birds of equal vertical range, one in the lower part of a mountain mass and the other in the upper, the latter will be subjected to somewhat greater changes of temperature. But in Usambara this generalisation is modified by the special local effect of the scarps, where the same minima×altitude gradient is maintained as on the plateaux, but the maxima fall off with abnormal rapidity. As a result the temperature range at altitudes falling within the Intermediate Zone does not exceed that in the Lowland.

If we take the standard climates only, without reference to eco-climatic modifications, we find that in the Lowland Zone, i.e. up to 2500 ft., the temperature ranges from 34° C., the hot season maxima at the bottom of the zone, to 15° C., the cold season minima at the top, conveniently expressed as 34 / 15° C., a range of 19° C. In the Intermediate (East Usambara) the range is 28 / 10° C. = 18° C., in the Highland, 26 / 0° C. = 26° C.; from the bottom of the Lowland to the top of the Intermediate it is 24° C., from the bottom of the Intermediate to the top of the mountains it is 28° C., and from top to bottom of the mountains some 34° C.

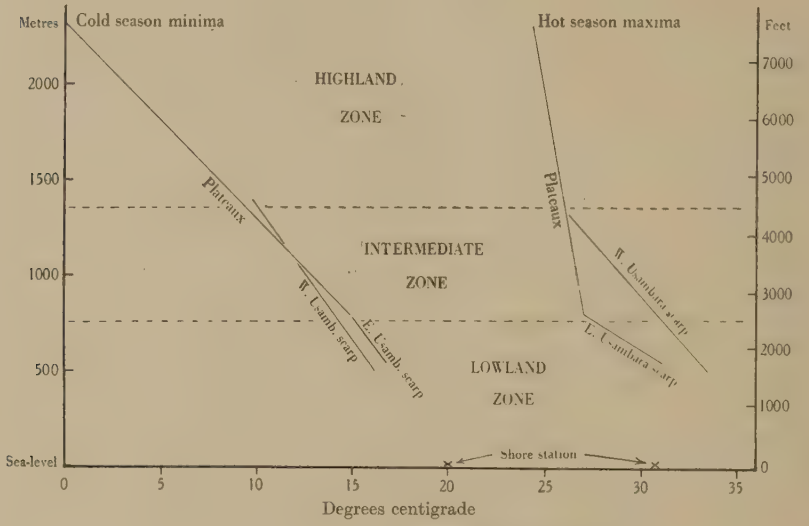

Fig. 1. Temperature × altitude gradients in Usambara.

It will be observed that the temperatures at either extreme are far from lethal. The maximum of 34° C. is lower than the summer maxima over a good deal of the earth's surface. Frost is unknown until above 5000 ft. At 6200 ft. the lowest record obtained in a screen is only −3° C.

Standard temperature figures cannot be quoted as the temperature range of any species of bird without taking account of the eco-climatic modifications resulting from its habitat. There is evidence (Moreau, 1935*b*) that the maxima in the eco-climate of the ground-stratum of Evergreen Forest run 3 or 4° C. lower than the standard, though the minima are the same. On the other hand bare ground, low grass and unshaded bushes get hotter in the day and colder at night than the standard. The actual differences are very variable: for a basis of argument we can take them as being in the neighbourhood of 5° C., more or

less, in both directions. Therefore an individual bird living in bushes under the forest canopy will encounter maxima some 8° C. lower than an inhabitant of bushes in a contiguous clearing, and its total temperature range will be some 13° C. less.

The only bird eco-climates we know anything about are those mentioned above, namely the equable climate in the undergrowth of the Evergreen Forest and the extreme climate in grass etc. The other eco-climates, mainly in tree-tops and in bushes with a certain amount of overhead shade, probably approximate more nearly to the standard climate than do the others. In any particular locality in the Lowland Zone individual birds whose habitats engender these three types of eco-climate are exposed to the following temperature ranges: equable, 34 − 4 / 16 = 14° C.; standard, 34 / 16 = 18° C.; extreme, 34 + 5 / 16 − 5° = 28° C. That is to say, individual birds living in extreme eco-climates are habituated to a temperature range nearly twice as great as the others. But, as species, the birds exposed to an extreme eco-climate do not show any greater adaptability to the changing temperature conditions of altitude than do the others; for, as has been shown, exceedingly few birds of any kind extend throughout all three zones; and among these birds there is no significant difference between the number of species in each eco-climatic category.

The temperature ranges experienced by individual birds of the Highland species are greater than those in the Lowland, amounting at the highest altitudes to 25 − 4 / 2 = 19° C. in the equable eco-climate, 25 / 2 = 23° C. in the standard, and 25 + 5 / 2 − 5 = 33° C. in the extreme. The widest temperature tolerances will of course be exhibited by those species which range through all three zones and whose habitats engender extreme eco-climates. Of all the local birds probably none surpasses the pipit, *Anthus richardi lacuum*, in its temperature range, for it is found at sea-level and in the highest clearings, always on short grass. Its range is at least 34 + 5 / 0 − 5 = 44° C.

It is noteworthy that the temperature difference between the top of the Lowland Zone and the bottom of the Highland is only about 4° C. in maxima and 6° C. in minima. But this narrow gap is bridged by very few of the species, although, as calculated above, individual birds in all zones and all eco-climates show temperature tolerances from two to six times the width of the gap. It is emphasised again that the zonal limitations are found to operate without distinction upon every category, ecological or phylogenetic, in this numerous and highly heterogeneous population.

We know exceedingly little about the significance of any particular element of natural temperature in bird life, but Kendeigh (1932) has established experimentally that the behaviour of Sparrows and House-wrens resident in the North Temperate Zone is not disturbed by rising air-temperature until 93° F. (= 34° C.) is reached. 34° C. is considerably higher than the maximum standard temperature (28° C.) at the lower edge of the Intermediate Zone, the level below which with few exceptions the Highland and Intermediate fauna

fails to pass; it is very much higher than the maximum at that level for the equable eco-climate species, which is $28-4=24°$ C.; and it is actually no higher than the maxima of the extreme eco-climate species, which is $28+5=33°$ C. Therefore unless our species belonging to the Highland plus Intermediate are more sensitive, and many of them very strikingly more sensitive, to high temperatures, than are the Temperate Zone species on which Kendeigh worked, the higher maxima at lower levels are not the direct bar to the downward extension of the high-level species.

As regards the low-temperature relations of birds, Kendeigh (1932) finds that the average night temperatures combined with the number of hours of darkness, when the procuring of food is usually impossible, are crucial factors in distribution. "This is particularly true of the smaller passeriform species. Larger and heavier birds may have a greater resistance to low temperatures"—which would be expected on elementary physical grounds.[1] But if we refer to the lists of birds given in the sub-section "Vertical Range" as occurring from Lowland to Highland throughout, we find, among both the eleven Forest species and the ten other species, birds of every size, from the 500-gm. Francolin[2] down to the 7-gm. Waxbills[3] (two species). We do not in fact find the size discrimination that we should expect if temperature minima were generally effective in determining distribution.

The suggestion (Moreau, 1934, p. 57) that temperature might have a direct influence on the rate of reproduction was at the time it was written purely speculative and tentative, only based on analogy with insects. Since then Baker and Ransom (1932) have shown experimentally that cold diminishes the fecundity of voles (*Microtus*) and Huxley and Howard (1934) have quoted field observations showing that cold interferes with, and ultimately inhibits, the coitive process in coots (*Fulica atra*), a phenomenon they term "diserotisation". In these instances the degrees of cold concerned were greater than those encountered in Usambara by day at any elevation, but it would not be surprising if tropical animals had a comparatively high threshold in this respect. The breeding seasons in the area are complicated. For our present purpose it suffices to observe that breeding maxima do not generally coincide with the hottest months, and in many species the breeding impulse appears to take its rise during the coldest. Thus the maxima of the cold months might be relevant in controlling distribution.

As would be expected, on plotting these maxima on Fig. 1 we get temperature × altitude gradients approximately parallel to the hot season maxima. The temperatures run about 6° C. lower throughout. It is obvious that if specific temperature thresholds for normal coition do exist at high enough levels to be

[1] Within our area the duration of darkness factor is practically a constant for season, for locality and of course for altitude; only as between equable eco-climate birds and others it is different, because under the Forest canopy darkness reigns for an hour longer out of the twenty-four than in the open.

[2] *Francolinus squamatus usambarae.*

[3] *Spermestes n. nigriceps*; *Estrilda astrild minor.*

of practical importance under local conditions, then the difference in maxima, amounting to 9° C., between the equable and extreme eco-climates would be important in restricting extreme eco-climate birds to the appropriate habitats.

As will be seen from the figure, the characteristic of the local temperature × altitude gradients is the abnormally rapid falling off of the maxima on the scarps, which occur between about 1500 ft. and 4000 ft. (This is doubtless to be explained on general physical grounds.) Attention must be drawn to the fact that it is in this interval, where the maxima fall off most rapidly, that the most abrupt and extensive change takes place in the composition of the fauna. In assessing this generalisation some allowance would, however, need to be made for the influence of the topography; between at least 1500 and 3000 ft. the ground is everywhere so excessively steep that circumstances of soil and exposure introduce further variables. It appears also to be true that in the same critical interval the vegetation alters its specific composition rapidly while retaining a similar aspect. In fact the abrupt change in the avifauna takes place *pari passu* with an abrupt change in flora, as well as in temperature maxima. The problem whether the avifaunal change is due to the biotic or the climatic factor remains unsolved.

I have remarked that there appears to be practically no change in species' altitude limits with the seasons, and that the difference between the mean maxima of the hot months and of the cold months is about 6° C. The temperature × altitude gradients being what they are, in the cold season a Highland bird would have to move down several thousand feet and an Intermediate bird from the top to the bottom of the scarps, to offset the seasonal fall in temperature, and *vice versa*. Certainly if the birds had specific "preferenda" and made any serious attempt to follow them, their vertical movements with the seasons should be well marked. As they are not, it becomes unlikely that a direct reaction of birds to temperature is a general factor in controlling distribution locally.

(*c*) *Subjective factors.*

In discussing Biotic Factors above, the conclusion was reached that only in a small minority of species could the presence or absence of the prime requirements in type be considered as adequate to explain the observed distribution. It is unnecessary to quote a list of species whose limitations appear to be peculiarly facultative, but there is one group of birds to which reference must be made in this connection.

It is not surprising that the bird communities inhabiting the bushes beneath the canopy of Evergreen Forest and those of the bushes under the open sky in Savannah country, should have practically no species in common. I have described (1935) the differences that exist between the two formations in temperature and in light intensity as well as in the aspect and specific composition of the vegetation. With all these obvious environmental differences

we are very ready to assume that each of the two habitats must possess its specific bird fauna, even though we cannot say which of the several variables is the determinant. Between the canopy of Evergreen Forest and the tree-tops of Savannah the environmental differences are not so great. Although the Forest canopy is never denuded of leaves, its surface is subjected to the same insolation as the tree-tops in the Savannah. Yet the Savannah species of Barbets, the two Savannah Wood-Hoopoes, the Savannah Starlings, the Savannah Turacos and Parrots, and the Savannah *Batis*—a list not intended to be exhaustive—apparently never think of entering the canopy of Evergreen Forest, although the essential requirements of these birds are all supplied in greater abundance in a given area of Forest than in Savannah. In fact, most of the Savannah species mentioned have congeners filling identical niches in Forest. But the abundance displayed in Forest goes untapped and unrecognised by these Savannah birds, which in captivity or when exotic trees are present take to strange foods with facility. The instance thus derived from a whole category of birds must raise a doubt whether the difference between the fauna of bushes in Savannah and the fauna of bushes under the Forest canopy, which we may well assume to be due to physical variables in the environment measurable and appreciable by us, might not be due, at least in part, to imponderable subjective factors.

In the same way, when we consider the tree-haunting fauna of the Semi-humid Savannah and that of the Semi-arid Acacia Thorn-bush, we cannot find biotic or eco-climatic factors to account for more than a small part of the enormous specific difference between them.

A relevant general observation has been made in the Semi-arid area of Usambara, where an expanse of very dry Thorn-bush is traversed by a swampy river valley utilised for growing quantities of rice. Great numbers of birds batten on the rice, but all belong to species that are characteristically associated with swamp vegetation or rank grass. It appears in fact that these birds eat the rice because it has been planted where they are accustomed to forage. On the other hand several species of seed-eating birds inhabit the Thorn-bush, actually within sight of the rice-fields, but apparently seek no food there and do not even make occasional foraging raids over the intervening few hundred yards, although at the season when the rice is ripe the amount of seed available among the thorn-bushes appears to be at a low ebb. This has been confirmed by stomach examination, for which I am indebted to Mr W. Nowell.

I referred above to the fact that many forest species are never observed in either introduced plants or regenerating growth in clearings, although food, if not nesting sites, is available in type. A good example is afforded by *Dicrurus l. ludwigii*, the Forest Drongo, with quite unspecialised feeding and nesting habits. It will cling to the scantiest vestiges of primary Forest, but has never been noted in plantation trees, where *Dicrurus adsimilis divaricatus*, its

Savannah congener, makes itself at home. That such a preference as this may be psychological is suggested by observations on the Weaver, *Ploceus bicolor kersteni*, which ranges through the mid-stratum of Evergreen Forest, vestigial and secondary as well as primary, and shows a special partiality for lianas. It feeds on a great variety of insects (as shown by stomach examinations) mostly taken from 20 to 100 ft. above the ground. It has been found in a group of only three or four Forest trees with a draping of lianas, but not in exotics of any kind, however tall or densely planted, except in one patch of *Pithecolobium dolce*. These are trees less than 20 ft. high, of open growth, and resembling in general aspect Savannah trees rather than the species' normal haunts; but this *Pithecolobium* is unique among the Amani plantations in being heavily laced with lianas.

It is certainly remarkable how birds of highly discontinuous geographical range are found to occur, even in their extreme localities, in particular environmental relations where the biotic factor cannot be invoked as responsible. For example:

(1) In the Usambara Lowland Forest a number of species of birds occur that are characteristically West African, but are separated from their congeners by the mass of mountain and semi-desert that fills practically the whole of East Africa. The climate resembles that of parts of West Africa inhabited by the species in question, and in the same formation certain plants of West African affinities also occur: but it is impossible to believe that the specific composition of the available food is responsible for the appearance of these birds, for they include such miscellaneous feeders as *Illadopsis rufipennis distans*, an example of whose stomach contents has been listed in a footnote on page 176.

(2) A South African Pipit, *Anthus lineiventris*, is recorded by Shelley (1900) as "frequenting rocky hillsides especially where a stream issues from the rock" in the Transvaal. The bird reappears in Usambara, after an immense interval of space; and here also it occurs in exactly similar situations, but in the Intermediate Zone, with a climate somewhat different from that in its South African localities.

Where plant associations are concerned the idea has been gaining ground among ecologists that the animal community should not be regarded as merely parasitic upon, or existing within the matrix of, the vegetation with which it is found, but rather that the animal and plant communities form one biotic entity. Phillips (1931) has given a convenient summary of this view. In his phrasing, the biotic communities are constituted by interdependent organisms, including all forms of plant life, "with integrated responses, reactions and co-actions". Such a view appears to require a long and close association between the components of the biome, in the course of which their mutual bonds, none the less lasting because we fail to define their nature, have been forged and riveted. This implies concurrent evolution of the components of the

biome, difficult to envisage in Usambara with its interpenetrating biota and comparatively small Forest islands. The historical factor is thus introduced, and it is desirable to discuss it.

(*d*) *The historical factor.*

It appears from information kindly supplied to me by Dr P. R. Lowe (*in litt.*) that many of the existing genera of birds date at least from the Oligocene and that not a few species are as old as the beginning of the Pleistocene. For Africa itself little material is available, but there is reason to suppose that the generalisation holds good. Evidence has lately been accumulating that the Pleistocene in Africa, as elsewhere, was a period of great climatic oscillation, and enough data exist for the biotic effects to be sketched (Moreau, 1933*b*).[1] The position is then, that throughout the Pleistocene different climatic types were successively dominant and the existing families of birds, if not in all cases the actual genera, were being subjected for long periods to the resulting different environments. A further factor of general import was introduced by the configuration of Africa, which appears to have been essentially a continent of two levels since the period of differential uplift at the close of the Tertiary. Eastern, Central and Southern Africa is mainly a peneplain—of which such mountains as the Usambaras are detached blocks—over 3000 ft. above the sea. Western Africa, the coastal portion of East Africa, and the country connecting them on the north are low-lying. Thus within the limits of Tropical Africa two main divisions have consistently provided for evolution two somewhat differentiated theatres, each of wide extent.

The climatic impulses to evolution have come from two pluvials, each succeeded by a dry period, the second of which East Africa is still undergoing. The first (Kamasian) pluvial was long and severe, lasting probably down to 400,000 years ago. Evergreen Forest and a lowered temperature must have been the dominant conditions over the whole of Tropical Africa. It is probable that the present Highland Zone conditions existed throughout the Central African peneplain, an area compact enough and large enough for the evolution of the specialised and now extremely discontinuous Highland Forest biome. Concurrently the Lowland Forest biome could have been developing in an unbroken belt, round the north end of the elevated peneplain, from the Atlantic to the Indian Ocean. The succeeding dry period may have been hotter or colder than the present. If it were colder, conditions favourable to the development of the existing Highland non-forest fauna would have been dominant over the peneplain, with the forest restricted to isolated areas of higher rainfall, as at present. The second (Gamblian) pluvial was nearly as intense as the Kamasian, again with lowered temperature, though of less duration, and may have come to an end only some 22,000 years ago. The Forest predominance of the early

[1] The conclusions there arrived at have been accepted in the most recent review of the evidence (Wayland, 1934).

Pleistocene was re-established, and during a second extended period the specialisation of the Forest biome could be confirmed. Meanwhile the dry-country biota must have survived only on the fringes of the Forest or in local rain-shadows; but since the end of the Gamblian the positions have been reversed and the Evergreen Forest is in its turn vestigial.

It will be observed that both the Forest and the dry-country biota were favoured by two stadia in which the predominance of one or the other appears to have been sufficiently long and complete for specialisation to take place in practical isolation. The indications are that since the beginning of the Pleistocene the Forest dominance has on the whole been considerably the longer; and this might account for the higher degree of specialisation in the components of the forest biome and the greater adaptability shown, as mentioned under "Field Observations", by Savannah birds.

Bates (1930, p. xviii) remarks that in West Africa the birds of the "second growth in the forest are for the most part not birds of the forest" but "peculiar kinds found nowhere else". He comments that this only goes to "prove man's system of clearings ancient enough to have produced special kinds of birds". In East Africa it is also true that the birds of regenerating forest are not the birds characteristic of the full primary forest. But they do flourish on the edge of primary forest, apparently foraging outwards or upwards and treating the dense tangle of the forest edge as their refuge and home, while a few of the species are also inhabitants of the tall dense clumps of bush found in a certain type of savannah. Personally I find it impossible to connect the evolution of these forest-edge or second-growth species with the activity of man. Recent excavations have given grounds for the belief that man has lived in East Africa since the beginning of the Pleistocene. But it would be going beyond the evidence of archaeology to believe that he practised agriculture at any early stage in his development. I have been unable to find any definite pronouncement on the antiquity of agriculture. But it does not appear to have been practised until Neolithic times, the beginning of which in the Fayum of Egypt has been dated to about 6000 B.C. by Gardiner (1929). Less than 10,000 years would therefore be available as the time allowance for the evolution of a number of species of different genera, associated, moreover, with many distinctive plants: and not many of us would consider that adequate. The difficulty of clearing primary rain-forest with primitive tools must also be borne in mind. And the wide geographical range of several of the forest-edge species makes impossible demands on the activity of early African man. In my view, conditions favourable to the development of the secondary and forest-edge species ruled throughout the periods of active advance and retrogression of Evergreen Forest, when peninsulas and islands of richer growth, especially in valleys, must have exposed a great length of marginal conditions.

4. Usambara facts and some generalisations.

It is the intention in this section not to attempt to frame generalisations but to discuss how the Usambara data given above square with suggestions and hypotheses advanced by other workers.

(*a*) *Humidity and vegetation.*

"The distribution of birds in South-West Africa is governed largely by rainfall: altitude seems scarcely to play any part as a barrier" (Reviewer of de Schauensee, 1932). "The faunal areas [of the Congo] differ in the amount and distribution of the rains, and sometimes in the temperature." "In the lowlands of the Congo the climate seems to affect the birds mainly through the vegetation it determines" (Chapin, 1932, p. 81).

In Usambara the fauna shows a high degree of variation with the amount of rainfall. The Semi-arid Thorn-bush fauna shares only 20 per cent. of its species with the Semi-humid, and the Humid (Forest) fauna is totally different from either. But the botanical difference is apparently no less great, and it is impossible to say how far there may be any direct influence of humidity on bird distribution. We have what might be indications, but they do not point in the same direction.

(1) A few species characteristic of the Lowland Semi-humid miss the Intermediate (all types of climate) and reappear in the Highland Semi-humid.

(2) Six Lowland Semi-humid species extend into the clearings in the Intermediate Semi-humid but not into those in the Intermediate Humid, against two common in the latter and not observed in the former.

In both (1) and (2) the temperature and the vegetation in the two areas frequented by each species is somewhat different. The degree of humidity is the most constant element in the environment.

On the other hand:

(3) Where Evergreen Forest exists in both the Humid and Semi-humid areas of the same zone, the latter possesses no peculiar species of birds, most being common to both.

(4) Where, owing to edaphic factors, similar vegetation is enabled to exist in three different climatic types, the composition of the bird-fauna is also similar.

Chapin (1923) finds that "avifaunal lines are never more sharply defined than the changes of composition and habit of the vegetation". On Usambara data we can certainly agree with this statement so far as changes in composition of the vegetation are concerned; but it does not hold good for the habit of the vegetation. In Evergreen Forest, areas of identical "habit" may be found housing the very different Lowland and Highland faunas.

(*b*) *Temperature.*

"Temperature alone seems to exert no marked influence on the distribution of animal and plant life until an elevation of 5000 ft. is reached." "It is probable that mountain-dwelling birds dislike the heat of the lowlands, while the majority of lowland birds avoid the cold of altitudes above 6000 ft." (Chapin, 1932, p. 81.) "The influence of temperature on African bird distribution has been underestimated. Beside Alpine and Temperate Zones on the isolated mountain tops, an extensive Subtropical Zone is recognised. The mean annual isotherm of 70° F. [=21° C.] serves roughly as the boundary between this and the Tropical Zone, but a Transition Zone of varying width, wherein an overlap of the two avifaunas occurs, is recognised." (Bowen, 1933, pp. 269, 270.)

In Usambara there are three well-marked zones: the Lowland, with upper limit of 21° C. annual mean (extremes about 34 / 15°); the Intermediate, which is faunistically transitional, though it appears to possess two peculiar species, with upper limit at 18° annual mean (extremes about 26 / 10°); and the Highland. Thus, if temperature is of direct significance, it asserts itself in Usambara so low as 2500 ft.

At first sight the strict zonation seems to afford clear evidence of the direct influence of temperature. This is supported by several facts:

(1) My zonation and the temperature at the upper limit of my lowest zone, arrived at by independent personal investigations in an area where the temperature × altitude relations are abnormal, coincide strikingly with Bowen's, arrived at by a general review.

(2) The same species tend to appear at lower altitudes in Usambara than on other mountains, where the temperatures are higher than in Usambara at the same altitudes.

(3) The same species reappear in a most remarkable way at the same altitude on detached blocks of the Usambara Mountains.

(4) Above a certain limit the Highland Forest species inhabit communities of dissimilar aspect, so that the temperature is the obviously constant element in their environment.

But on the other hand:

(5) As in the case of humidity, concurrently with the changes in temperature changes are going on in the botanical composition, and the question whether the zoological changes are directly dependent on the one or the other is open.

(6) To a postulate that the effect of temperature is direct, the corollary is that in Usambara differences so small as 2 or 3° C. must be sufficient to bring about a general change in the fauna; and must be operating with equal effect on birds habituated individually to ranges of as much as 27° C. and as little as 13° C.

(7) Notwithstanding the degree of sensitiveness thus postulated, there is no vertical movement with the changing temperatures of the seasons.

(8) No hypothesis of the direct effect of temperature can be accepted without an indication of what elements in natural temperatures are effective. In Usambara it appears probable from Kendeigh's experiments (1932) that with Highland birds the maxima at their lower limits are not high enough, and with Lowland birds the minima at their higher limits are not low enough, to provide barriers.

(9) The observational data would be consistent with a hypothesis that the lower maxima at higher altitudes were inhibitory to Lowland birds, possibly owing to "diserotisation". (Blank-Weissberg (1932) has put forward a view that specific summer maxima may be effective in determining range.) On this hypothesis the eco-climatic difference, amounting to 9° C., between the maxima in the equable and the extreme habitats might be effective in keeping non-Forest birds out of Forest; but if this were a prime factor in distribution, Lowland equable birds might be expected at higher altitudes to emerge from the Forest undergrowth into situations where they could get higher day maxima. Of this there is no evidence.

(*c*) *Subjective factors.*

"They [birds] choose their own home." "Many of the important phyla of birds have plainly evolved in continuous relation to certain types of environment." (Chapin, 1932, pp. 263, 264.) "Each species selects its ancestral habitat, instinctively recognising it by the conspicuous, not necessarily the essential, features." (Lack, 1933.)

Much of the Usambara distribution appears to be explicable only by subjective factors. This is supported particularly by the following facts:

(1) Rich feeding grounds in immediate proximity are avoided.

(2) Past conditions in Africa have been such as would admit of the prolonged evolution of the several main biota under observation.

On the other hand:

(3) The hypothesis of habitat selection can hardly be said to offer a real explanation. Factors that can be defined and measured must always be preferred to it and sought exhaustively. For it must be remembered that an array of distributional problems similar to those encountered among birds is presented to us by plants; some, intensively studied, have been solved; and in any case no factor on a psychological plane can be admitted for plants.

(4) In any species for which "habitat selection" is put forward to explain an observed distribution an attempt must at least be made to define the particular environmental element that satisfies its selectiveness. In Lack's studies of English birds on Breckland plantations the most obvious variable of the habitat was usually height of vegetation. In most of the Usambara instances

I have given above where adherence to particular habitats cannot be rationalised, there is some obvious superficial difference between the habitats affected and those avoided, e.g. in non-Forest, differences in type of ground-cover. But some of the different Evergreen Forest communities with different faunas, e.g. the Intermediate at 3000 ft. and certain areas of the Highland at 6000 ft., resemble each other remarkably in general aspect, although hardly at all in specific botanical composition. If we sought to admit the hypothesis of habitat selection in these cases also, we should have to postulate further that the birds' criterion is not merely facies, but something more minute, perhaps even the specific pattern of their surroundings.

5. Conclusion.

In conclusion I can only say that after all this talk, and after observing and meditating upon bird distribution in a limited area for more than five years I am still hardly any nearer to a rational explanation of it than I was at the beginning. Especially does this apply to the surprising faunal transitions within a few miles of where I am living, on the edge of the East Usambara plateau. If I were called upon to declare my convictions in the matter I could only say that temperature and humidity have a lot to do with it, but I cannot decide how; that vegetational formation, itself largely dependent on geomorphology as well as on both temperature and humidity, is a prime indicator and prime determinant of the bird population in any particular spot; but that vegetational *composition* within the *formation* is far less important. I should have to add that the only reason I can suggest, except in a small minority of species, for the association of particular birds with particular communities of plants is constantly being rejected, even by myself, as no true reason, although I perceive dimly how the close associations that so astonish us may have had their roots in the past.

I have tried to consider this whole problem with as open a mind as possible. As a result I find myself in the deplorably confused and negative position I have indicated. I should like to quote from David Garnett in a review of a biological work that is as tendentious as only devotion to a single-factor explanation can make it:

"There is nothing the mind of man hates more than for two causes to combine and co-operate to produce one effect. Sometimes, indeed, two causes must be admitted to exist, but then, asks man, which is the chief? It is natural enough that he should prefer one, since if he has only one, he can get a lot of fun out of it, particularly in applying it where it doesn't seem to fit; whereas if he has a dozen or more equal and irreducible causes, he will feel very sorry for himself and will excite pity and derision in the critics who read his books or listen to his arguments."

6. Summary.

The data subjected to analysis here are derived from several years' field observations and collecting in Usambara, crystallised in synecological and autecological studies available elsewhere. The local distribution of about 300 species is sufficiently well known to be utilised.

Field observations are given in generalised form under Horizontal and Vertical Ranges. The dichotomy between the Forest and non-Forest faunas is so profound that these have to be dealt with separately.

The generalised facts thus obtained are considered in relation to Biotic, Climatic and Subjective factors as defined previously (Moreau, 1934). Finally the Usambara data are related to the various hypotheses that have been put forward by other workers as to the relative significance of environmental variables in determining bird distribution. A list of reasons is given for and against each hypothesis.

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AN ECTOPARASITE CENSUS OF DUCKS AND GEESE (ANATIDAE) IN UGANDA

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Through the kindness of the Imperial Institute of Entomology I am having the opportunity of studying an extensive collection of ectoparasites, containing representatives of all groups of the ectoparasitic Arthropoda, which is being made by Mr G. H. E. Hopkins and his colleagues of the Agricultural Laboratories, Uganda. I should like to take this opportunity of expressing my indebtedness to Mr Hopkins for the careful way in which he is carrying out his part of the work.

As far as I am aware no complete census of the ectoparasites of birds has yet been published, although more recently parasitological surveys have been done on mammals (e.g. Pearse, 1929; Elton and others, 1931). Waterston (1914) published a paper on the Mallophaga of the genus *Philopterus* (= *Docophorus*) occurring on British auks, and in this he gives a census of the species of this genus found on individual birds. Ewing (1931) writes on the taking of an ectoparasite census of five classes of vertebrates, including birds, and the value of such a work, but he deals mainly with the hosts of chiggers, and as noted in his summary the report is only preliminary. No detailed account is given of the ectoparasites of birds. In my paper (1934) I gave a summary of the ectoparasites found on eight British birds representing as many species.

The birds of Uganda are being dealt with in groups, namely, Anatidae, Numididae, Musophagidae, etc. This paper deals only with the ducks and geese (Anatidae); the remaining groups will be dealt with as the material is worked out.

The methods used by Mr Hopkins are as follows: each bird is placed in a bag as soon as possible after it is shot and the bag is carefully sealed; these bags, each containing a single bird, are taken to the laboratory and both bag and bird are carefully examined and every kind of parasite is collected (with the exception of the Analgesidae, etc.). The entire collection from a single bird is placed in a tube of approximately 70 per cent. alcohol together with the necessary data. In a few instances the parasites from more than one specimen of the same host have been placed together in a single tube. The parasites collected contain representatives of the following groups: Mallophaga (bird-lice), Hippoboscidae (bird-flies), Ixodoidea (ticks), Siphonaptera (fleas). In the case of the Anatidae only the Mallophaga were represented in great numbers, one specimen of a tick occurred and a few odd specimens of fleas.

Table 1. *Census of the ectoparasites.*

Species of bird	No. of specimens of bird examined	Genera of Mallophaga: *Trinoton* spp. ♀♀	*Trinoton* spp. ♂♂	*Trinoton* spp. imm.	*Acidoproctus* spp. ♀♀	*Acidoproctus* spp. ♂♂	*Acidoproctus* spp. imm.	*Anaticola* spp. ♀♀	*Anaticola* spp. ♂♂	*Anaticola* spp. imm.	*Menopon* spp. ♀♀	*Menopon* spp. ♂♂	*Menopon* spp. imm.	*Anatoecus* spp. ♀♀	*Anatoecus* spp. ♂♂	*Anatoecus* spp. imm.	Total No. of parasites: Mallophaga	Ixodoidea	Siphonaptera
Sarkidiornis melanotus (Penn.)	6	4	2	2	—	1	—	3	6	6	2	—	—	1	1	—	65	1*	—
(Knob-billed goose)	7	6	4	4	—	—	—	7	3	6	—	—	1	4	1	1			
Nyroca erythrophthalma (Weid.) (African pochard)	5	1	1	—	1	—	—	10	8	—	2	—	—	—	—	—	23	—	—
Plectropterus gambensis gambensis (Linn.)	5	9	2	19	98	91	198	31	21	10	166	159	128	—	—	—	955	—	1†
(Spur-winged goose)	1	—	—	—		23‡													
Dendrocygna fulva (Gmel.)	14	2	4	2	2	2	—	—	—	—	—	—	—	—	—	—	250	—	—
(Whistling teal)	12	4	3	5	8	4	—	—	—	—	—	—	—	—	—	—			
	11	10	10	23	39	35	64	—	1	1	10	7	11	2	—	1			
Dendrocygna viduata (Linn.) (White-faced duck)	7	11	9	7	24	16	73	—	—	—	9	5	1	—	—	—	155	—	2§
Alopochen aegyptiacus (Linn.) (Egyptian goose)	5	—	1	3	40	29	34	15	15	9	3	3	1	—	—	—	153	—	—
Anas querquedula Linn. (Garganey teal)	3	2	3	1	—	—	—	15	10	19	2	—	—	1	—	—	53	—	—
Anas undulata undulata Dubois. (Yellow-billed duck)	10	2	2	1	—	—	—	20	29	49	—	—	—	—	—	—	103	—	—
Nettapus auritus (Bodd.) (Pigmy goose)	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

* One ♀ of *Haemaphysalis leachii* (Audouin). This species of tick is common and widely distributed in Africa.
† One specimen of *Ctenocephalides felis strongylus* (Jordan)—an obvious straggler.
‡ For some unknown reason the condition of the Mallophaga off this host was such that a determination of the sexes, etc., was impossible.
§ Specimens of *Xenopsylla* sp.—obvious stragglers.

Table 2. *Percentage occurrence of Mallophaga on the birds.*

Name of bird	Genera of Mallophaga				
	Trinoton spp.	*Acido-proctus* spp.	*Anaticola* spp.	*Menopon* spp.	*Anatoecus* spp.
Sarkidiornis melanotus (Penn.)	33·8	1·6	47·7	4·6	12·3
Nyroca erythrophthalma (Weid.)	8·7	4·4	78·2	8·7	0
Plectropterus gambensis gambensis (Linn.)	3·2	42·9	6·5	47·4	0
Dendrocygna fulva (Gmel.)	25·2	61·6	0·8	11·2	1·2
Dendrocygna viduata (Linn.)	17·4	73·0	0	9·6	0
Alopochen aegyptiacus (Linn.)	2·6	67·3	25·5	4·6	0
Anas querquedula Linn.	11·3	0	83·0	3·8	1·9
Anas undulata undulata Dubois.	4·5	0	95·5	0	0
Nettapus auritus (Bodd.)	0	0	0	0	0

Mr Hopkins tells me that during the time that the parasites of the Anatidae were being collected there was a rat-flea survey being carried out in the same laboratory and therefore the three specimens of fleas were obvious stragglers on the birds from rats.

Each specimen will in time be determined to species; but for the present they have only been determined generically, as I have noted during the counting of the material that only one species of each genus of Mallophaga appears to be present on a single host species. In Table 1 a summary of the numbers of each sex of the adults of each species of Mallophaga is given and also the number of immature specimens whose sex is indeterminable. A detailed table of the number of each sex, etc., of the species of Mallophaga found on individual birds will be deposited in the Zoological Library of the British Museum of Natural History for future reference.

Altogether 97 birds representing 9 species of Anatidae have been examined, and the total number of parasites obtained from these birds is 1759. The figures given in the tables will not be discussed until the remaining groups have been worked out. Five genera of Mallophaga are represented among the parasites, and of these, species of the genera *Trinoton* and *Anatoecus* are found only on ducks, geese and swans; *Acidoproctus* and *Anaticola* are found only on ducks and geese; the genus *Menopon* in its present status contains species found on a very wide range of hosts.

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THE ANIMAL POPULATION OF A MEADOW NEAR OXFORD

By JOHN FORD.

(*With Plate* 6 *and* 3 *Figures in the Text.*)

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1. Introduction.

An investigation of the fauna of the soil and vegetation of certain areas in a meadow lying between Wytham and Cumnor Hills, half-way between Botley and Eynsham, and about three miles from Oxford, was made in the winter and spring of 1931–2 and the spring of 1933. This meadow had not been touched for over three years, and in consequence was covered by a thick mat of vegetation and rotting grass. Its general situation (May 1929) is shown in the photo (Pl. 6). The soil is a heavy clay and, except in the summer months, is very damp and, in places, water-logged. The sod is seldom deeper than 6 in., and below this depth only a few organisms were found. In area about 5 acres, this field is transversed by five ridges, about 1 ft. higher than the intervening hollows. The vegetation is typical of grassland in the district, and there was in progress an invasion of blackthorn from the surrounding hedges. At the western end of the field is a small stream, while the northern edge is bounded by a strip of woodland in which elm is dominant.

The larger inhabitants of the meadow were not investigated. They included the field vole (*Microtus agrestis hirtus*) and the mole (*Talpa europaea*), while rabbits (*Oryctolagus cuniculus*) inhabited the woodland strip bordering the field. During the summer frogs (*Rana temporaria*) were abundant, while various birds, including song thrush (*Turdus ericetorum*), blackbird (*T. merula*), robin (*Erithacus rubecula*) and hedge-sparrow (*Prunella modularis*) were commonly present.

This paper does not attempt to estimate the actual population of the whole field, but to give a measure of the *real density* of population in a certain set of habitats in that field, namely, the ridges, from which alone samples were taken.

2. Methods of sampling.

Thompson (**10**) demonstrated that a 9-in. cube, as used by her and Morris (**7**, **8**, **9**), was the most satisfactory size for soil samples, from the point of view of statistical accuracy. For the following reasons, neither the size of the samples as used by these workers, nor their methods of extracting the fauna, were practicable:

(*a*) The mean population of a 9-in. cube of Botley soil is at least four times as great as that obtained by Thompson. As a result of this, it is impossible to evaluate a sample of that size before certain changes set in, due to evaporation of water, which cause the clay to set in a hard brick (see Buckle (**1**)).

(*b*) The glutinous nature of the clay prevented the use of sieves, as considerable pressure of water was required to fragment it.

The sample used was 3 in. square and 9 in. deep and was cut from a larger block of soil in the laboratory. The sample was cut into $\frac{1}{2}$-in. layers, representing successive depths, and each layer was broken up with stout needles under water. All tracheate animals and Collembola floated to the surface and were counted as they were picked off; while small worms, Enchytraeidae and Nematodes, could be seen and obtained while swimming about. Large Oligochaetes were counted before immersion. The process was continued, with changes of water, till no further organisms appeared and the soil was reduced to a fine silt.

For the collection of surface forms, 6-in. square areas of soil were skinned and the vegetation placed on a Berlese funnel. Hand collections were also made in the field.

3. The population census: quantitative.

Table 1 summarises the densities of different orders of animals in the soil and surface vegetation. The numbers of each order collected in all samples is given, together with the calculated density expressed as numbers per acre. The mean number of organisms per sample of soil ($3 \times 3 \times 9$ cu. in.: 16 samples) was 378, with a standard error of $\pm 13{\cdot}6$ per cent. The mean number of organisms per sample of surface vegetation (6×6 sq. in.: 12 samples) was 51, with a standard error of ± 10 per cent. The combined population density of both surface and soil animals in the ridges amounted to 272, 569, 440 per acre, the standard error of the mean being ± 12 per cent.

Comparisons with populations of other districts. At Rothamsted Morris (**8**) recorded a population of 15,100,955 individuals per acre in soil dressed annually with farmyard manure, in which the Collembola, amounting to 2,390,570 per

acre were the third largest component. The most numerous group was the Enchytraeidae, 3,609,424 per acre, while the second largest was the Formicidae (ants) with 2,946,125 per acre. These figures are of the same order of magnitude as those for the Botley population density, with the exception of the Collembola. Excluding Collembola from the Botley population we get 23,870,880 individuals per acre as compared with 12,710,385, which is the total Rothamsted population, also excluding Collembola.

Table 1.

Order	Soil population		Surface vegetation population	
	Total No. collected	No. per acre	Total No. collected	No. per acre
INSECTA:				
Collembola	5507	239,884,920	111	1,611,720
Thysanura	8	348,480	—	—
Coleoptera	29	1,263,240	40	580,800
Larval Elateridae	31	1,350,360	—	—
Hemiptera	—	—	7	101,640
Hymenoptera	—	—	16	232,320
Diptera	—	—	6	87,120
Larval Cecidomyidae	—	—	11	159,720
Thysanoptera, Lepidoptera and Psocoptera	—	—	7	101,640
Larvae and pupae unidentified	47	2,047,320	54	784,080
ARACHNIDA:				
Acarina	171	7,448,760	140	2,032,800
Araneidae	—	—	28	406,560
Opiliones	—	—	7	101,640
MYRIAPODA*	41	1,785,960	27	392,040
ISOPODA:				
Oniscoidea	40	1,742,960	73	1,059,960
OLIGOCHAETA:				
Lumbricidae	53	2,308,680	24	348,480
Enchytraeidae	66	2,847,960	30	435,600
MOLLUSCA:				
Snails	7	304,920	18	261,360
Slugs	—	—	6	87,120
NEMATODA	55	2,395,800	—	—
PLANARIA	—	—	2	29,040
Totals	6055	263,755,800	607	8,813,640

* For the purposes of this calculation the old grouping of Symphila, Diplopoda and Chilopoda under the name Myriapoda has been retained.

The difference in these totals is mainly due to a population of 7,448,760 Acarina per acre at Botley as compared with 531,986 Acarina at Rothamsted. Assuming the arable land on which Morris worked to have formed a homogeneous habitat, these differences may be accounted for in the following ways: (*a*) The presence of abundant vegetation at Botley provides a far greater food supply than could exist in manured arable land; this, incidentally, probably also accounts for the preponderance of Acarina. (*b*) The loose open soil at Rothamsted, by facilitating the evaporation of water, is not advantageous to Collembola. (*c*) It is probable that the comparatively large population of ants at Rothamsted is responsible for the exclusion of other organisms. (At Botley

Formicidae were uncommon, only one small nest, containing some 300 individuals, was found. It has not been included in the quantitative census.)

The populations investigated by Thompson at Aberystwyth appears to be of the same order of magnitude as those obtained by Morris, although she does not give sufficient data to determine them. They occurred in pasture-land and Collembola formed their largest component.

More recently, Trägårdh (**11**) has reported a population in the soil of a spruce forest which has a magnitude approaching that now under discussion. He obtained a mean population of 120,000 Collembola in a cubic metre of soil, with a maximum sample of 282,500 per cu. m. Assuming the Botley population to occupy the soil above a depth of 6 in., one obtains a population per cu. m. of approximately 388,000 Collembola. The approach of the spruce forest soil population to that at Botley becomes considerably closer when examined from the point of view of *total density*, since the Collembola of the spruce forest are living in association with an equally great Acarine population.

4. The population census: qualitative.

The following is a list of the species obtained in the area investigated. Since many species occur both in the soil and in the surface vegetation, all are included together, with short notes opposite each group to indicate the most usual habitat. S.=in soil; V.=in surface vegetation; Y.=active throughout the year.

Species	Notes
INSECTA	
Collembola	
Hypogastruridae	
Pseudachorutes subcrassus Tbg.	S., Y.
Onychiuridae	
Onychiurus armatus Tbg.	S., Y.
Tullbergia quadrispina Börn.	
Isotomidae	
Isotoma minor Schffr.	S.
I. violacea Tbg.	S., V.
Folsomia quadrioculata Tbg.	
Entomobryidae	
Lepidocyrtus lanuginosus Tbg.	On V. *O. villosa* disappeared in Nov., reappearing in nymphal state in May
Orchesella villosa Geoff.	
Heteromurus nitidus Templ.	
Sminthuridae	
Sminthurus viridis L.	On V. Disappeared in Nov., reappearing in nymphal state in May
Thysanura	
Campodea staphylinus Westw.	S., Y.
Campodea sp.	
Psocoptera	
Sp. indet.	One specimen. V.
Thysanoptera	
Sp. indet.	V.
Lepidoptera	
Sp. indet.	Larvae in S.
Larvae, spp. indet. (5)	

Species	Notes
HEMIPTERA HETEROPTERA	All Hemiptera were found on V. during spring and summer
Reduvidae	
Nabis major Cost.	
Capsidae	
Megaloceraea erratica L.	
Miris calcaratus Fall.	
HEMIPTERA HOMOPTERA	
Delphacidae	
Stenocranus minutus Fab.	
Kelisia vittipennis Fieb.	
Jassidae	
Limotettix 4-notata Fab.	
Athysanus sordidus Zett.	
Thamnotettix crocea H.-S.	
Aphididae	
Sp. indet.	
COLEOPTERA	
Staphylinidae	
Tachyporus chrysomelinus L.	Staphylinidae were found in S. and on V. throughout
T. atriceps S.	Y. *L. longulum* and *L. geminum* as well as species
Stenus clavicornis Sp.	of the genus *Stenus* occurred as frequently at a depth
S. ossium S.	of 1½ in. as on the surface
S. lustrator Er.	
S. flavipes S.	
Lathrobium longulum Gr.	
L. geminum Kr.	
Quedius rufipes Gr.	
Sipalia circellaris Gr.	
Tachinus rufipes D.G.	
Phloeobium clypeatum Ml.	
Gabrius sp.	
Atheta sp.	
Scydmaenidae	
Tychus niger Pk.	S. and V.
Silphidae	
Phosphuga atrata L.	S. near surface and on V.
Catops chrysomeloides Pz.	
Choleva angustata F.	
Ptinidae	
Ptinus tectus B.	This species probably introduced from neighbouring houses
Hydrophilidae	
Cercyon melanocephalus L.	S. and V.
C. pygmaeus Il.	
Megasternum boletophagum Mm.	
Lathridiidae	
Enicmus histrio Jy.	V.
Trichopterygidae	
Trichopteryx sp.	S.
Curculionidae	
Apion virens Hb.	V.
Otiorrhynchus ligneus Ol.	
Sp. indet.	
Sp. indet.	
Carabidae	
Clivina fossor L.	S.
Stomis pumicatus Pz.	
Pterostichus diligens St.	
P. strenuus Pz.	
Bembidion sp.	
Elateridae	
Agriotes sp.	As larvae, S.
Also various unidentified Coleopterous larvae	

Species	Notes
DIPTERA	Diptera occurred on V. An undetermined species of Sphaeroceridae occurred constantly throughout the winter among the leaf bases of grasses
Sepsidae	
Sepsis cynipsea L.	
Opomyzidae	In 1933, following the introduction of cattle, *Scatophaga stercoraria* L. (Cordyluridae) appeared
Balioptera tripunctata Fln.	
B. combinata L.	
Drosophilidae	
Drosophila sp.? *fenestrarum* Fln.	
Drosophila sp.	
Cecidomyidae	
Sphaeroceridae	
Chironomidae	
Tipulidae	
Larvae Cecidomyidae	
Larvae unidentified	
HYMENOPTERA	
Formicidae	
Myrmica ruginodis Nyl.	One ant's nest was found, containing rather more than 300 individuals. Both brachypterous and normal forms of *I. latrator* (13 specimens) were found hibernating in this nest. (The brachypterous form is var. *means* Grav.) *B. ruficornis* was also found hibernating in the soil
Ichneumonidae	
Ichneumon latrator F.	
Hemiteles sp.	
Hemiteles sp.	
Braconidae	
Blacus ruficornis Nees.	
ARACHNIDA	
ARANEIDA	Spiders occurred on V., rarely in S. Most species appear to be active throughout the winter
Clubionidae	
Clubiona sp. (? more than one species)	
Thomisidae	
Xysticus sp.	
Oxyptila trux Bl.	
Pisauridae	
Pisaura mirabilis Clk.	
Lycosidae	
Pirata latitans	
Trochosa terricola Sh.	
Trochosa sp.	
Tarentula pulverulenta Clk.	
Lycosa tarsalis	
Lycosa sp.	
Lycosa sp.	
Dictynidae	
Dictyna sp.	
Argiopidae	
Neriene rubens Bl.	
Erigone atra Bl.	
Centromerus bicolor Bl.	
Bathyphantes gracilis Bl.	
Linyphia clathrata Sund.	
Pachygnatha clerkii Sund.	
P. degeerii Sund.	
Araneus sp.? *cornutus* Clk.	
Aprolagus beatus Camb.	
OPILIONES	
Phalangidiidae	
Oligolophus tridens C.L.K.	V.
Nemastomatidae	
Nemastoma lugubre O.F.M.	V.
ACARINA	
Oribatidae	
Hoplophora dasypus Dugés.	V., and in top ½-in. layer of S. More rarely in deeper soil to 2 in. *H. dasypus* and *O. orbicularis* were the dominant spp.
Oribata orbicularis Koch.	
O. globula Nic.	
O. lucasii Nic.	
Cepheus tegeocranus Herm.	

Species	Notes
Gamasidae	
Veigaia cervas Oudms.	
Gamasus sp.	
Trombidiidae	
Allotrombidium sp.	
Trombella sp.	
Uropodidae	
Uropoda sp.	
CRUSTACEA	
ISOPODA	
Oniscoidea	
Armadillidium vulgare Latreille	V., excepting *T. pusillus* which occurred in S. Y., but in cold weather tending to form aggregations. *P. muscorum* is the dominant sp.
A. pulchellum Zenck.	
Trichoniscus pusillus Brandt.	
Philloscia muscorum Scopoli.	
MYRIAPODA	
CHILOPODA	S. and V., except Symphyla which occurred only in S. The Chilopoda is the dominant order. Y.
Lithobiidae	
Notophilidae	
DIPLOPODA	
Julidae	
Polydesmidae	
SYMPHYLA	
OLIGOCHAETA	
Lumbricidae	Generally in soil. Lumbricidae occasionally were found at a depth of 8 in., but more usually above 4 in. The small white Enchytraeidae were sometimes found crawling on grass. Y.
Enchytraeidae	
NEMATODA	S. Two types were present; one, small and transparent, was fairly frequent, the other, larger and opaque, very rare. Y.
MOLLUSCA	V., but snails occasionally in S. *A. agrestis* was the most abundant mollusc
Agriolimax agrestis L.	
Slugs. Spp. unid. (3)	
Snails. Spp. unid. (4)	
PLANARIA	
Tricladidae	
Rhynchodemus sp.	2 specimens found on grass

The total number of species in the above list is 132. This figure is evidently less than the real number of species in the population, since the Oligochaeta and Myriapoda are not identified. The springtail *Onychiurus armatus* represents approximately 60 per cent. of the total Collembola population and is thus the most abundant species. *Lepidocyrtus lanuginosus* and *Heteromurus nitidus* are the most numerous of the surface Collembola.

The majority of the soil Collembola are saprophagous, living on the humus, of which, owing to the thick, uncut and damp grass of the Botley field, there is a plentiful supply. MacLagan (6) has remarked that the role of Collembola in soil formation has been underestimated, it being next in importance to that of earthworms. Certain species, of which *Smynthurus viridis* is one, are phytophagous, and gnaw at the epidermis of grasses and other plants. *Smynthurus viridis* has been observed feeding on grasses at Botley, and it appears to be most active at night.

Parasitisation of Collembola by Nematodes, as reported by Morris and Thompson, has been observed, in the present case, in *Isotoma violacea*, the parasite protruding dorsally between the abdominal segments.

With regard to number of species, the Coleoptera (beetles) is the best represented order, with 34. 14 species belong to the family Staphylinidae, of which those of the genera *Stenus*, *Lathrobium* and *Tachyporus*, all occurring frequently in the soil, prey upon Collembola.

It may be noted that no adult Elateridae were found. The larval life of the species of *Agriotes* is exceptionally long, in some five years, and, in consequence, the excess of larval forms over adults is exceptionally great.

The Araneidae (spiders) is the next most widely represented order, with 21 species. They include the genera *Xysticus*, *Erigone*, *Linyphia* and *Pachygnatha* which are among the most effective predators of Collembola. The dominant species are probably *Pachygnatha degeerii* and *Pisaura mirabilis*; it is difficult to be certain of this owing to the habit of certain species, when immature, e.g. *Clubiona*, of forming aggregations which cause an apparent dominance.

The Acarina (mites), the second largest component of the population, are represented by 10 species. These are mainly phytophagous and saprophagous and are most abundant in the top $\frac{1}{2}$-in. layer of soil, from which they ascend into the thick mat of rotting grass which covers the field.

Comparison with species found in other districts. In considering the qualitative aspect of the census, a comparison of the species obtained with similar lists from other districts shows that, although the composition of various faunas may differ greatly, there tends to be a correspondence between the total number of species. This has been pointed out also by Elton (**5***a*). Table 2 shows the number of species of the four principal arthropod orders, Collembola, Coleoptera, Araneida and Acarina, at Botley, compared with the totals of species of the same orders at Aberystwyth (pasture-land) and Rothamsted (arable with manure), together with the total numbers of species of all other orders. It should be recalled that the Rothamsted population was living in soil with no surface vegetation. The presence of grass and other plants on pasture-land and meadows probably accounts largely for the extra species at Botley and Aberystwyth.

Table 2.

	Numbers of spp. at			Botley spp. which also occurred at	
Order	Rothamsted	Aberystwyth	Botley	Rothamsted	Aberystwyth
Collembola	14	25	10	6	3
Coleoptera	31	35	34	1	4
Araneida	5	4	21	—	1
Acarina	13	19	10	—	1
Other orders	41	57	57	8	6
Totals*	104	140	132	15	15

* The three figures, 104, 140 and 132 are approximate. In no case were identifications complete and probably the real total in each case is larger than that given.

Photo. C. Elton

Phot. 1. Pasture field in which the soil survey was done.

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5. Depth distribution of the soil fauna.

The depth to which soil organisms penetrate depends upon the depth at which food, either the roots of plants or humus, is found and upon the lightness or heaviness of the soil. Histograms representing the depth distribution of the Botley soil fauna take similar forms to those given by Morris, Thompson and others for various localities; but owing to the compact nature of the soil they are vertically compressed when compared with those obtained in lighter soils or in arable land (Fig. 1). Save for an occasional Lumbricid, no organisms were ever found below a depth of 8 in. and very few below $4\frac{1}{2}$ in.

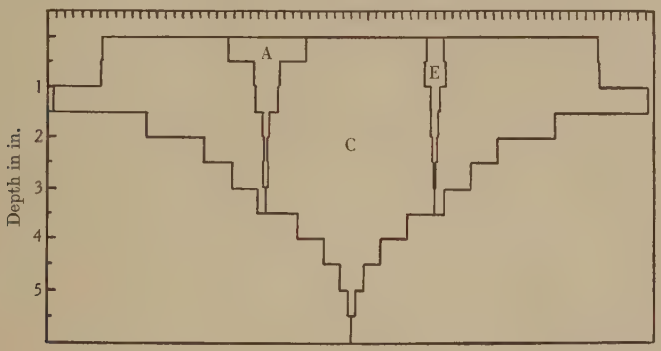

Fig. 1. Depth distribution in mean soil sample ($3 \times 3 \times 9$ cu. in.) of Collembola (C), Acarina (A) and Enchytraeidae (E). (1 horizontal division = 1 individual.)

6. Soil water.

Estimations of the water content of three samples were made in December. Weighed amounts from each $\frac{1}{2}$-in. layer, freshly cut, were dried in an oven at 105° C., cooled in desiccators, and the loss of water found on reweighing.

It was found that whereas, at successively greater depths, the Collembola increased in number down to the $1\frac{1}{2}$-in. level, and below that decreased, the water content decreased continuously from the surface downwards. Although the Collembola are dependent for their existence on a minimum supply of water in the soil, since they die rapidly in drought, there is probably no direct relation between the water content, when above that minimum, and the numbers of Collembola. An exception to this occurs when the water is present in gravitational form instead of the more usual capillary and hygroscopic forms. For their continued existence Collembola need to live in contact with a film of water (**4**), and this is supplied, in favourable conditions, by capillary and hygroscopic water in the soil.

When, in late spring, the soil begins to dry, there is probably a downward migration to the damper levels at greater depths (Thompson (**10**)). A histo-

gram of the depth distribution of Collembola in May, compared with histograms for the winter months, shows a greater population below $1\frac{1}{2}$ in. than above (Fig. 2). This may, however, be partly due to the mortality of organisms above that level being greater than that below it.

7. Effects of moles and cattle.

It is known that the presence of gravitational water in the soil is deleterious to its population. Edwards (**5**) notes that ground water has the effect of expelling air from the soil and also that it renders organisms more liable to fungal attacks. In alluvial soil he found that the organisms were confined almost exclusively to the top inch, probably owing to the high water level in a low-lying situation.

Among 16 samples, 15 of which yielded normal counts, was one, taken in November, in which the Collembola only numbered 44, as against a mean of

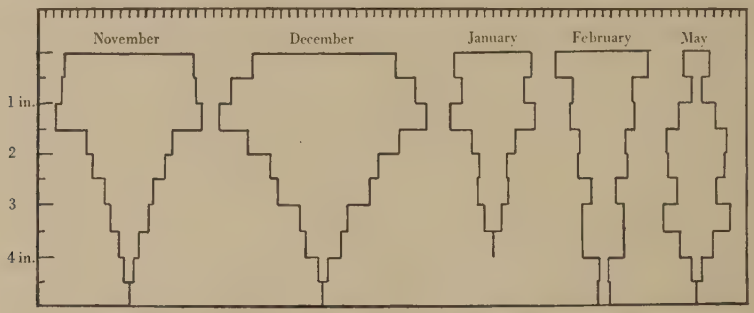

Fig. 2. Monthly depth distribution of Collembola. (1 horizontal division = 5 individuals.)

344 per sample, with all other organisms, excepting 5 Acarina, absent. This sample may be considered abnormal, since it falls below the standard error of the mean, which is ± 51 or 15 per cent. It had been cut from a position adjacent to the burrow of a mole (*Talpa europaea*), and, on inspection, it was found that the soil was in a peculiar state, known, I am told by Mr Clarke of the School of Rural Economy, as "puddled". Soil adjacent to other burrows was found, in wet weather, to be in a similar condition. In damp weather, when there is an abundance of capillary water in the soil, mechanical action of sufficient violence has the effect of disturbing the soil particles so that the water fills the pore spaces between them, producing a sort of mud from which air is excluded.

In order to discover exactly the effect of puddled soil on the behaviour of Collembola, some *Onychiurus armatus* were placed on a piece of soil in this condition. It was found that they were quite incapable of burrowing, and wandered about helplessly. On a piece of normal soil they responded immediately with a negatively phototropic reaction and, by making use of the pore

spaces, entered the soil. Also, if holes were made with needles in the surface of the puddled soil, they entered these immediately.

It would thus appear that any puddling of the soil would hinder the progress of organisms such as the soil Collembola which dwell in the pore spaces and, at the same time, would tend to cause death by drowning. It is probable that where there is a large population of burrowing mammals, puddling, in damp weather, destroys a considerable number of soil organisms. In confirmation of the above, a second sample was taken from soil puddled by cattle. It contained only 57 Collembola, 3 Acarina, 1 Staphylinid beetle and 2 Myriapoda (Notophilidae). It has been shown by Thompson (**10**), Morris (**7**) and others that the soil of fields open to grazing cattle has a definitely smaller population than that in fields in the same locality not grazed.

8. Seasonal fluctuations of the soil population.

Thompson (**10**) showed that the soil population fluctuates seasonally, having a maximum in December or January and a minimum in April or May,

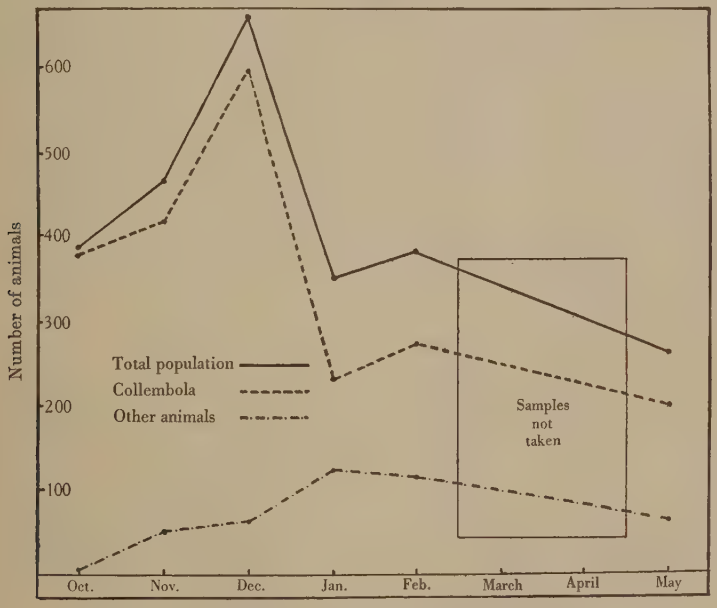

Fig. 3. Mean monthly soil populations. Botley (1931–1932).

the number of individuals increasing through the autumn and decreasing through the spring. She also demonstrated that this fluctuation was due almost entirely to the Collembola and that the populations of other organisms

remained fairly constant throughout the year, but with slight increases in spring and early winter.

Fig. 3 shows the fluctuation of the soil population at Botley during the winter of 1931–2. There is a definite peak in December, both in the total population curve and in that for Collembola. There is a slight peak in the curve for the population of other organisms in January, but it is clear that the principal cause of the total population fluctuation at Botley, as at Aberystwyth, is the Collembola.

Edwards (**5**) gives a curve representing fluctuation in soil populations, also at Aberystwyth. The maximum population is given in October, but since the curve is based only on four samples, taken in January, July, October and again in the following January, it is possible that the real peak in numbers did not occur until after October. Again the Collembola were the principal cause of the fluctuation.

9. Acknowledgments.

I wish to thank Prof. E. S. Goodrich, F.R.S., for allowing me the facilities of the Department of Zoology and Comparative Anatomy at Oxford University. For help in identifying specimens I have to thank Mrs M. Hughes, Mr J. M. Brown, Dr A. R. Jackson, Mr A. W. Stelfox, Commander C. Walker and Dr B. M. Hobby—the latter also for much help and criticism; Prof. E. B. Poulton, F.R.S., for allowing me to use the type collections in the Hope Department; Mr C. G. T. Morison for allowing me the use of the laboratory in the School of Rural Economy; Mr G. R. Clarke, of the same school, for information on "puddling"; the Trustees of the Christopher Welch Scholarship for financial assistance; and finally Mr Charles Elton, without whose help this work could not have been attempted.

10. Summary.

1. An investigation was made of the animal population of the soil and vegetation of the ridges transversing a meadow which had remained untouched for three years.

2. The *total density* of population in the soil was 263,755,800 individuals per acre, of which over 90 per cent. were springtails (Collembola). The density of population in the surface vegetation, of all forms, was 8,813,640 per acre.

3. 132 species were taken from the soil and vegetation together. Remarkably few species are common with those in other areas surveyed in Great Britain, although there is a correspondence in the totals.

4. The majority of organisms occurs near the surface of the soil, the greatest concentration being in the layer between depths of 1 and $1\frac{1}{2}$ in. below the surface. Few organisms were found below a depth of $4\frac{1}{2}$ in. and none below 8 in.

5. Water content estimations at various levels showed no relation between the amount of water and the population at those levels, provided the water was in either the hygroscopic or capillary form. This does not hold good when the water content is below a certain minimum.

6. Soil "puddled" by moles or by cattle is responsible for the exclusion of organisms in the affected area.

7. The averages of samples taken in the winter months show a rising population to December and a falling one from January to May. This fluctuation is confined entirely to Collembola.

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THE GAPEWORM (*SYNGAMUS*) IN WILD BIRDS

By JAMES W. CAMPBELL.

1. Introduction.

During 1934 an investigation was carried out, in co-operation with the Oxford University Bureau of Animal Population, into the occurrence of gapeworms (*Syngamus*) in wild birds. Gapeworms have been recorded from a number of wild birds, and Cram (**1**) gives a list of 28 species from which gapeworms identical in structure with *Syngamus trachea* (Montagu)—the gapeworm causing epidemics amongst poultry—have been obtained. In addition to those species included by Cram, gapeworms have also been reported from the sparrow, linnet, martin, kestrel and pigeon. A different species, *Syngamus merulae* Baylis, occurs in the blackbird (*Turdus merula*).

The presence of gapeworms in wild birds is of practical importance, as Elton and Buckland (**2**) have pointed out in regard to the rook (*Corvus frugilegus*), on account of the possibility that birds may spread the parasite amongst poultry, and also for the part the parasite may play in checking the numbers of wild birds. But the part that wild birds play in spreading gapes amongst poultry and game is still undecided. A number of workers have shown that it is possible to infect chickens experimentally with gapeworms obtained from the rook, starling, pheasant, etc., and Clapham (**3**) has transferred *Syngamus merulae* from the blackbird to chickens. Taylor (**4**), however, working with *Syngamus* from starlings, obtained results which showed that, although the worms occurring in the starling and chicken are morphologically identical, physiological strains evidently exist, and that for this reason it is probable that wild birds do not play so important a role in spreading gapes as was at first expected. Taylor (**5**) discusses other factors which may tend to retard this spread of the parasite by wild birds.

I have to thank the Oxford University Bureau of Animal Population for assistance during this inquiry. The systematic work has been carried out at the British Museum (Natural History) by Dr H. A. Baylis, to whom I am also indebted for much help and advice. I also wish to thank all those who have helped in various ways, and especially the Earl of Eldon; Mr A. D. Middleton; Mr E. L. Taylor, who kindly carried out feeding experiments; and Captain H. B. Moser of the Imperial Chemical Industries Game Research Estate at Knebworth.

2. Previous investigations.

Lewis (**6**, **7**) found 14 out of 38 starlings examined infested, and subsequently out of 482 examined 35 per cent. infested. 128 of those infested contained only 1 pair of worms each, 41 had 2 pairs each, 9 had 3 pairs each and 4 had 5 pairs each. No details are given of the age of the birds, but there was evidence of a gradual increase towards March in the percentage infested.

Taylor (**4**) recovered 71 pairs of gapeworms from 356 starlings, and the percentage infested was about 19. Although the age of the birds was not noted, it was noticed during the latter part of the inquiry that immature birds only were infested.

During May 1928, Elton and Buckland (**2**) examined 41 rooks from the Oxford district. Out of 8 adult rooks examined, 4 were infested, while 31 out of a total of 33 young rooks (they had just learnt to fly) were infested (94 per cent.). In one case over 40 pairs of gapeworms were counted in an immature rook, and most of them were fairly heavily infested. In 2 of the adult rooks only one pair of worms was found, a condition not found in any of the young birds. It was suggested from these results that not only is the adult rook capable of acting as a carrier of the parasite, but that young birds which become infested when young gradually free themselves from gapeworms, as is the case in poultry.

Rice (**8**) examined 258 rooks, mainly young birds killed in May, and a tendency for the birds to free themselves from worms as they got older was noticed. During May 98 per cent., in June 85 per cent., and in August 62 per cent. were infested.

3. Results of the present investigation.

In 1934 a total of 1011 birds, belonging to 53 species, were examined. 11 species were found to contain gapeworms. 8 of these contained *Syngamus* morphologically identical with *S. trachea*:

Carrion Crow (*Corvus corone*)	Starling (*Sturnus vulgaris*)
Rook (*Corvus frugilegus*)	House Sparrow (*Passer domesticus*)
Jackdaw (*Colœus monedula*)	Purple Sandpiper (*Calidris maritima*)
Magpie (*Pica pica*)	Pheasant (*Phasianus colchicus*)

This is apparently the first record of the occurrence of *Syngamus* in the purple sandpiper: 7 were examined and 2 contained one pair of worms each. The birds were obtained on Boreray, a small island off the coast of North Uist (Outer Hebrides).

Three species contained worms identified as *Syngamus merulae*:

Song Thrush (*Turdus ericetorum*)	Blackbird (*Turdus merula*)
Redwing (*Turdus musicus*)	

Although Lewis (**6**) has recorded *Syngamus* from the song thrush, it was apparently *S. trachea*, so that this appears to be the first record of *S. merulae* in this species. It has also not been recorded previously in the redwing. It is interesting that members of the genus *Turdus* should be infested with *Syngamus* morphologically distinct from *S. trachea*, and further investigation would be desirable.

The totals of birds examined and the number found to be infested in each month, together with the total percentage infested for each species, are shown in Table 1. Since percentages based on relatively small totals are apt to be misleading, the actual totals are given in all cases.

Table 1. *Totals examined (E) and infested (I) in each month and percentage infested.*

Species	Jan. E.	Jan. I.	Feb. E.	Feb. I.	Mar. E.	Mar. I.	Apr. E.	Apr. I.	May E.	May I.	June E.	June I.	July E.	July I.	Aug. E.	Aug. I.	Sept. E.	Sept. I.	Oct. E.	Oct. I.	Nov. E.	Nov. I.	Dec. E.	Dec. I.	Total E.	Total I.	Percentage infested
Infested with *S. trachea*																											
Carrion Crow	—	—	—	—	—	—	4	0	—	—	7	4	—	—	—	—	—	—	—	—	—	—	—	—	11	4	36·3
Rook	5	1	2	0	7	2	10	2	129	121	1	1	—	—	—	—	1	0	1	1	—	—	—	—	156	128	82·0
Jackdaw	5	2	29	4	3	0	26	3	11	0	20	4	—	—	—	—	—	—	—	—	—	—	—	—	94	13	13·8
Magpie	—	—	—	—	1	0	4	1	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	6	2	33·3
Starling	28	5	17	3	8	1	30	6	5	1	6	1	2	0	2	0	—	—	5	0	5	2	3	1	111	20	18·0
House Sparrow	—	—	—	—	—	—	3	0	—	—	203	3	10	0	—	—	1	0	—	—	—	—	—	—	217	3	1·3
Purple Sandpiper	7	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	2	28·5
Pheasant	1	0	—	—	—	—	—	—	30	3	40	6	14	9	—	—	—	—	—	—	12	0	—	—	97	18	18·5
Infested with *S. merulae*																											
Song Thrush	4	1	4	1	8	0	—	—	11	1	3	1	2	1	—	—	—	—	—	—	—	—	—	—	32	5	15·6
Redwing	1	0	7	0	2	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	11	1	9·0
Blackbird	9	0	7	2	19	2	2	0	3	0	18	6	14	2	—	—	—	—	—	—	—	—	—	—	72	12	16·6

Table 2. *Totals of adults and immatures examined and infested and percentage infested.*

Species	Adults Examined	Adults Infested	Adults Percentage infested	Immatures hatched 1933 Examined	Immatures hatched 1933 Infested	Immatures hatched 1933 Percentage infested	Immatures hatched 1934 Examined	Immatures hatched 1934 Infested	Immatures hatched 1934 Percentage infested
S. trachea									
Carrion Crow	4	0	—	—	—	—	7	4	57·1
Rook	23	2	8·6	10	4	40·0	123	122	99·1
Jackdaw	38	2	5·2	37	8	21·6	19	3	15·7
Magpie	6	2	33·0	—	—	—	—	—	—
Starling	55	6	10·9	14	5	35·7	21	5	23·8
Pheasant	17	3	17·6	—	—	—	80	15	18·7
S. merulae									
Song Thrush	17	2	11·7	—	—	—	15	3	20·0
Redwing	11	1	9·0	—	—	—	—	—	—
Blackbird	41	4	9·7	—	—	—	31	8	25·8

Note. Age of 1933 hatched immatures approximately 8–10 months. No note was kept of the age of house sparrows examined. The 3 infested birds, all from Essex, each of which contained 1 pair of *Syngamus*, were 1 adult and 2 immatures. The age of 21 starlings, 4 of which were infested, was not noted.

The following species, of which no infested examples were obtained, were also examined. The figures in brackets are the number of each examined:

Jay (*Garrulus glandarius*) (31)
Greenfinch (*Chloris chloris*) (10)
Chaffinch (*Fringilla coelebs*) (14)
Little Owl (*Athene noctua*) (16)
Wood Pigeon (*Columba palumbus*) (12)
Common Snipe (*Capella gallinago*) (15)

Less than 10 each:

Hooded crow (*Corvus cornix*)
Twite (*Carduelis flavirostris*)
Linnet (*Carduelis cannabina*)
Yellow Bunting (*Emberiza citrinella*)
Reed Bunting (*Emberiza schoeniclus*)
Skylark (*Alauda arvensis*)
Rock Pipit (*Anthus spinoletta*)
Pied Wagtail (*Motacilla alba*)
Blue Tit (*Parus caeruleus*)
Coal Tit (*Parus ater*)
Marsh Tit (*Parus palustris*)
Golden-Crested Wren (*Regulus regulus*)
Whitethroat (*Sylvia communis*)
Fieldfare (*Turdus pilaris*)
Mistle Thrush (*Turdus viscivorus*)
Robin (*Erithacus rubecula*)
Hedge Sparrow (*Prunella modularis*)
Tawny Owl (*Strix aluco*)
Kestrel (*Falco tinnunculus*)
Common Buzzard (*Buteo buteo*)
Sparrow Hawk (*Accipiter nisus*)
Barnacle Goose (*Branta leucopsis*)
Brent Goose (*Branta bernicla*)
Wigeon (*Anas penelope*)
Common Eider (*Somateria mollissima*)
Red Breasted Merganser (*Mergus serrator*)
Stock Dove (*Columba oenas*)
Ringed Plover (*Charadrius hiaticula*)
Turnstone (*Arenaria interpres*)
Knot (*Calidris canutus*)
Dunlin (*Calidris alpina*)
Woodcock (*Scolopax rusticola*)
Common Gull (*Larus canus*)
Great Black-backed Gull (*Larus marinus*)
Moorhen (*Gallinula chloropus*)
*Common Partridge (*Perdix perdix*)

Table 3. *Adults and immatures. Number of pairs of* Syngamus *present in those examined.*

Species	Adults		Immatures 1933 hatched		Immatures 1934 hatched	
	No. of birds	No. pairs *Syngamus* each	No. of birds	No. pairs *Syngamus* each	No. of birds	No. pairs *Syngamus* each
S. trachea						
Carrion Crow	—	—	—	—	2	3
	—	—	—	—	1	2
	—	—	—	—	1	1
Rook	1	11	1	3	†Largest No. counted 66.	
	1	1	1	2	Only 2 out of 122 con-	
	—	—	2	1	tained 1 pair each	
Jackdaw	2	1	2	2	2	4
	—	—	6	1	1	2
Magpie	2	1	—	—	—	—
Starling	6	1	1	2	1	5
	—	—	4	1	4	1
Pheasant	1	6	—	—	‡1	26
	1	3	—	—	1	15
	1	1	—	—	1	8
	—	—	—	—	1	7
	—	—	—	—	1	5
	—	—	—	—	4	2
	—	—	—	—	3	1
S. nerulae						
Song Thrush	2	1	—	—	1	6
	—	—	—	—	2	1
Blackbird	2	2	—	—	1	7
	2	1	—	—	2	5
	—	—	—	—	3	2
	—	—	—	—	2	1

* Many partridges (*Perdix perdix*) and Red Legged Partridges (*Alectoris rufa*) examined by A. D. Middleton (unpublished) were infested.

† It was impossible in all cases to count the number of worms present. The majority were heavily infested. 30 birds counted yielded 357 pairs of *Syngamus*.

‡ In 3 young pheasants, the number of pairs of worms present was not noted.

Table 4. *The localities from which birds infested with* Syngamus *were obtained.*

Species	Locality	No. examined	No. infested
Carrion Crow (*Corvus corone*)	Layer Marney, Essex	9	4
	Longwood, Hampshire	2	0
Rook:	Layer Marney, Essex	1	0
Adult (*Corvus frugilegus*)	Tiptree, Essex	1	0
	Sampford Hall, Essex	2	0
	Abbotts Hall, Essex	1	0
	Bardfield, Essex	1	1
	Longwood, Hampshire	10	0
	Wickham, Hampshire	4	1
	Knebworth, Hertfordshire	3	0
Immature, 1933	Layer Marney, Essex	2	0
	Longwood, Hampshire	7	4
	Knebworth, Hertfordshire	1	0
Immature, 1934	Layer Marney, Essex	2	2
	Tiptree, Essex	1	1
	Sampford Hall, Essex	24	24
	Abbotts Hall, Essex	3	3
	Bardfield, Essex	39	39
	Horkesley, Essex	15	15
	Park Hall, Essex	21	21
	Wickham, Hampshire	2	2
	Knebworth, Hertfordshire	16	15
Jackdaw (*Colœus monedula*)	Layer Marney, Essex	8	0
	Great Lodge, Essex	5	0
	Longwood, Hampshire	51	8
	Knebworth, Hertfordshire	28	5
	Witchingham, Norfolk	2	0
Magpie (*Pica pica*)	Layer Marney, Essex	1	0
	Tiptree, Essex	3	1
	Longwood, Hampshire	2	1
Starling (*Sturnus vulgaris*)	Layer Marney, Essex	27	4
	Horkesley, Essex	1	0
	Longwood, Hampshire	54	11
	Knebworth, Hertfordshire	29	5
House Sparrow (*Passer domesticus*)	Layer Marney, Essex	91	3
	Longwood, Hampshire	126	0
Purple Sandpiper (*Calidris maritima*)	Boreray, North Uist	7	2
Pheasant (*Phasianus colchicus*)	Layer Marney, Essex	1	0
	Longwood, Hampshire	94	18
	Knebworth, Hertfordshire	2	0
Song Thrush (*Turdus ericetorum*)	Layer Marney, Essex	18	3
	Tiptree, Essex	3	1
	Longwood, Hampshire	11	1
Redwing (*Turdus musicus*)	Layer Marney, Essex	6	1
	Longwood, Hampshire	1	0
	Newton, North Uist	4	0
Blackbird (*Turdus merula*)	Layer Marney, Essex	31	5
	Tiptree, Essex	17	5
	Longwood, Hampshire	24	2

Throughout the inquiry, wherever possible, special attention was paid to the age of the birds examined and also to the number of worms they contained, in order to obtain evidence of any differences in the degree of infestation in adult and immature birds. In all the species where this was done not only was the percentage of immatures infected greater than adults but also as a rule they contained a larger number of worms. These results support the conclusions

of other observers that young birds tend to rid themselves of the worm as they get older, although adult birds are able to serve as carriers of the parasite. Full details both for birds infested with *S. trachea* and *S. merula* are shown in Tables 2 and 3. The localities in which infested birds were found are given in Table 4.

Owing to the ease with which immature rooks can be distinguished with certainty from adults until they are over a year old, the rook is one of the most suitable subjects for investigation. The young, 1934 hatched, rooks examined during 1934 were still being fed by their parents, and many of them had not yet learnt to fly. They were obtained from 8 different rookeries, 6 in Essex, 1 in Hampshire and 1 in Hertfordshire, so it is clear that gapes is widely distributed in rooks. It was impossible to count, in all cases, the number of worms present, but the majority were heavily infested and a number probably contained as many as the largest number counted. The general condition of the birds examined was good.

Elton and Buckland were of the opinion that in the rooks they examined the number of worms present (in one case over 40 pairs were counted) would not have impeded respiration, although the loss of blood might have been important. During 1934, it was noticed that there was considerable inflammatory reaction in the trachea of many of the young rooks. Although this was generally most marked in those containing numbers of worms, this was not always so, and it was quite as intense, in a few cases, in those containing relatively few worms. This factor would seem quite as important in embarrassing respiration, as the number of worms present. In several birds also, large ante-mortem clots, firmly attached to the trachea and containing remains of gapeworms, were found. In four cases there was a complete hollow "blood cast" lining the trachea to which it was attached.

It is curious that young jackdaws, many of which were obtained from the same localities as the young rooks, were not so heavily infested. The same feeding grounds are used and their food is very similar. It should be borne in mind, however, that young jackdaws are not hatched till several weeks after the majority of rooks. The young carrion crows were also birds still being fed by their parents; they had just learnt to fly. Two broods containing 3 and 4 birds respectively were examined and two from each brood contained gapeworms. The 3 adult pheasants containing gapeworms were wild birds which had been kept with others in a pen for nearly 2 months. They were picked out as suffering from gapes. Thus adult pheasants, unlike adult fowls, are able to act as carriers of the parasite. The young pheasants, whose ages ranged from 2 days to 2 months, were obtained from a rearing field in Hampshire. There was little evidence of inflammatory reaction in the trachea of those infected, a marked contrast to the condition found in the rook, but in two birds nodules similar to those described by Clapham (**3***a*) were present. Their general condition was poor.

A record was also kept of the position occupied in the trachea by the parasite, for Taylor (**4**) in 14 observations made during the experimental transmission of *Syngamus* from starlings to fowls found that *Syngamus* of starlings attached itself to the upper half of the trachea, whereas *Syngamus* of chickens made its attachment to the lower half. In view of this result, it was interesting to find that in the starling out of 17 pairs of worms, 12 were attached to the upper third of the trachea, 4 to the middle third and 1 was loose. In adult rooks out of 12 pairs of worms, 10 were attached to the lower third of the trachea, and in 29 pairs from pheasant chicks 20 were attached also to the lower third. In young rooks and the other species of birds examined no tendency for any particular region was noticed, worms occurring throughout the trachea. In three of the young rooks worms were found in the syrinx and once only in the bronchi.

In 1886 Walker (**9**) showed that the larvae of *Syngamus* occur in the earthworm, and it has been demonstrated since that earthworms are an important factor in the transmission of gapes. Clapham (**3**) carried out experiments which showed that *Eisenia foetida*, an earthworm found abundantly in decaying organic matter, is an important intermediate host of *Syngamus trachea*, and that *Lumbricus terrestris* is of less importance. Owing, however, to the somewhat restricted distribution of this earthworm and to the feeding habits of certain species of birds, it appears doubtful whether *Eisenia foetida* can be so important a factor in the transmission of gapes among wild birds as among poultry.

During the inquiry attention was paid to the occurrence of gapes amongst hand-reared pheasants. Feeding experiments were carried out by Mr E. L. Taylor with earthworms from a rearing field where, during the previous season, there had been heavy mortality from gapes. 92 earthworms—no *Eisenia foetida*—were divided amongst 8 chickens. At autopsy 2 chicks contained 1 pair of gapeworms each. Similar experiments were carried out for the field which was used subsequently for rearing during 1934. This had not been used for rearing purposes for at least 6 years. 293 earthworms—again no *Eisenia foetida*—were fed to 40 chicks, and at autopsy 2 were found to contain 1 and 6 pairs of gapeworms respectively.

From these results it is clear that a large number of earthworms would have to be consumed by the pheasant chicks before they became infested with gapeworms encysted in the earthworms.

4. Summary.

1. Gapeworms morphologically identical with *Syngamus trachea* were found in the carrion crow, rook, jackdaw, magpie, starling, house sparrow, purple sandpiper and pheasant.

2. Gapeworms identified as *S. merulae* occurred in the song thrush, redwing and blackbird.

3. Although the degree of infestation is lower in adult than in immature birds, adults are able to act as carriers of gapes. Young birds tend to free themselves from the worms as they get older. This confirms the conclusions of previous observers.

4. Gapes is widely distributed amongst rooks, for young birds from 8 different rookeries were found to be heavily infested.

5. There is a tendency for *Syngamus* in starlings to be attached to the upper third of the trachea, and to the lower third in adult rooks and pheasants.

6. Chickens were infested by feeding with earthworms obtained from a rearing field where pheasants had been reared.

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FLOOD MOVEMENTS OF THE LITTORAL FAUNA OF WINDERMERE

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(*With 2 Figures in the Text.*)

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1. Introduction.

Windermere is an oligotrophic lake with typical steep sides and narrow littoral region. At the north-west end the lake is backed by mountains which rise to 830 m. (2700 ft.), forming an extensive watershed with a steep "run off". The country south-east of the watershed is drained by two main streams, the Rothay and the Brathay, which unite a quarter of a mile above the lake. Cunsey Beck and Troutbeck, together with a few more small streams, also flow into the lake. The watershed gets rapidly saturated, and the surplus water drains away into the streams which rapidly become flooded and raise the level of the lake.

A preliminary account of some characteristic littoral animal communities of Windermere has already appeared (Moon, 1934), and further investigations are in progress. In making these studies certain lines of evidence have suggested that the fauna is constantly moving about the shore. Some of the most striking evidence of these movements is afforded by response to changes in the lake level brought about by floods. Detailed observations have been made on these movements, the results of which are recorded here.

2. Methods and records.

General proof of the movements of the fauna can, of course, be obtained when purely aquatic species are found on a recently inundated area. In this paper, however, the records given are quantitative. Quantitative results were obtained either by means of a specially designed scoop (Moon, 1935) which

took up a known sample area of the lake shore, or more frequently by trays bearing stones or other substrata from which all animals were previously removed. These trays were placed in rows along the lake shore vertical to the shoreline and left for the flood to cover. At the peak of the flood they were lifted out and the fauna removed. Usually a pair of control trays was lifted out at more frequent intervals and were placed further up the shore after the fauna had been removed from them. In this way it was possible to obtain information about the intermediate stages of the flood.

The changes in lake level were measured on a calibrated post in the laboratory boathouse. The level of the lake was read twice a day, in the morning

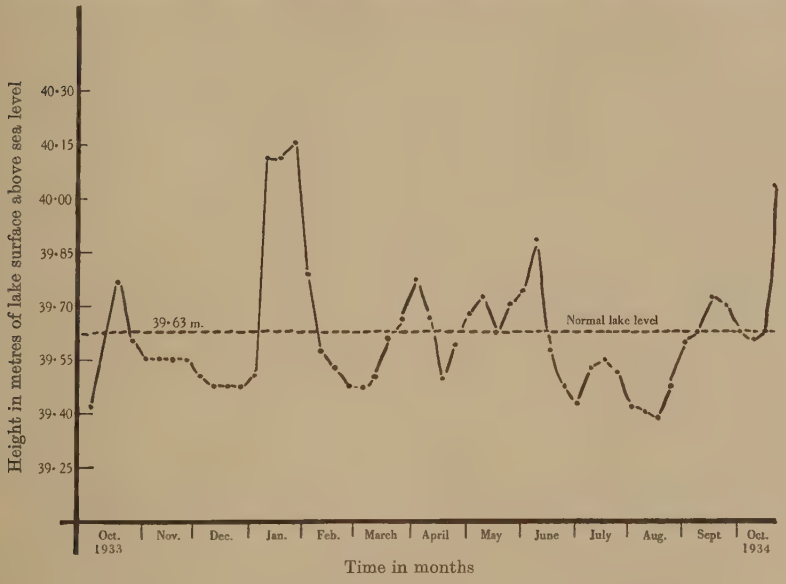

Fig. 1. Mean weekly variations in lake level, October 1933–October 1934.

and evening, and also before each collection. In this way it was possible to work out how long the places from which the collections were made had been covered by the rise in lake level. The following example shows how this was done:

Level of lake surface above sea level at time of collection = 39·5 m.

Depth at which collection was made = 7·5 cm.

The depth at which the collection was made is subtracted from the lake level, 39·5 m. − 7·5 cm. = 39·42 m.

An examination of the lake level records shows that 18 hours previously the lake was 39·42 m. above sea level. Therefore the collection was made at a place which began to be covered by the flood about 18 hours previously.

In this paper the term flood is taken as meaning any change in the level of the lake however small that change may be. The level of the lake has not been recorded for a sufficient length of time to determine what is the normal level of the water. But the arrangement of the terrestrial vegetation, particu-

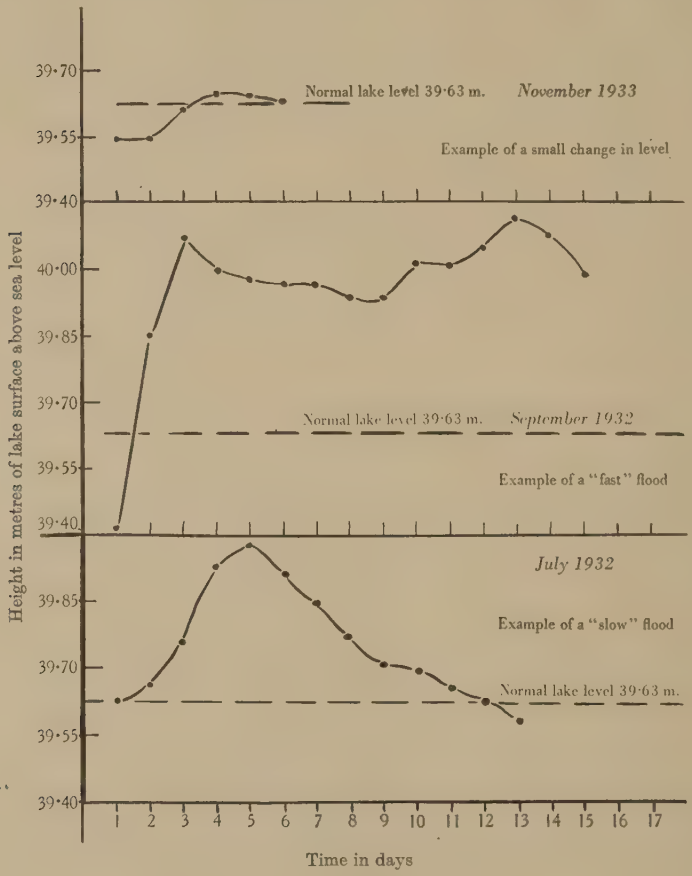

Fig. 2. Different types of flood.

larly the sharply marked line of mosses on inclined rock slopes, indicates that the normal level of the lake is 39·63 m.

In Fig. 1 the changes in lake level are given from October 1933 until October 1934. It will be seen that continual changes in level are taking place and that for considerable periods the lake was below normal level. This low level of the lake was due to long periods of drought.

Floods may be classified roughly into two types. Those which rise rapidly to a peak and then subside, and those which rise to a peak and do not subside for a long period. The former are characteristic of summer, the latter of autumn and winter, where a long period of rainfall maintains the high level of the lake. As well as the big changes of level there are many minor fluctuations, but even these cause movements of the littoral fauna. Despite the comparative insignificance of the small changes of level, their influence on the fauna is as pronounced as in the case of big flood. Fig. 2 shows three floods at different times of the year.

3. Rate of movement over flooded areas.

The level of the lake may rise rapidly, but usually the fauna can keep pace with the rising water. In Table 1 the rapidity of this movement can be seen. These figures represent collections made on a typical boulder shore. In other parts of the lake a rise in level of a few inches covers areas of grass or woodland quite unlike the substratum which the fauna normally inhabits. Even under these circumstances, however, some of the fauna moves over the flooded area. This is shown in Table 2.

Table 1.

Depth (cm.)	5	30	5	Lake edge	10–12·5
Locality	Epley Head	Bay III	Epley Head	Epley Head	Epley Head
Date	30. 7. 32	31. 7. 32	11. 11. 33	10. 10. 33	11. 10. 33
Area (sq. dm.)	9	9	18	18	18
Time covered (hours) ...	6	24	16	8	30
Ecdyonurus sp.	2	10	.	.	30
Coenis sp.	.	.	.	.	2
Centroptilum sp.	1	.	1	.	.
Isopteryx sp.	.	.	1	.	7
Nemura sp.	.	.	1	.	.
Limnophilius rhombicus	.	1	.	.	.
Stenophylax nigricornis	.	.	12	.	17
Elmis (adult)	.	.	.	.	1
Haliplus sp.	.	.	.	.	1
Hydraena gracilis	3	.	.	.	.
Chironomid sp.	3	.	.	1	2
Sigara minutissima	.	.	.	.	2
Gammarus pulex	.	9	12	52	5
Haemopsis sanguisuga	.	.	.	1	2
Planaria lugubris	.	.	.	.	1
Diplodontus decipiens	.	.	.	.	1
Polycelis nigra	.	1	.	.	.
Total of species	4	4	5	3	12
Total of individuals	9	21	27	54	71

At first sight it may seem that colonisation of these areas does not occur as rapidly as on boulder shores. It must be remembered, however, that areas of this type are usually associated with silted and sheltered shorelines, unfavourable for *Ecdyonurus*, *Isopteryx* and *Gammarus pulex*, which are the important colonisers of a boulder shore.

The rate at which colonisation takes place will obviously vary according to the rate at which the water rises. In the usual flood there is a change in

Table 2.

Locality	Congo, 15 cm.	Congo, 5 cm.	Pull Wyke, 5 cm.	Pull Wyke, 20 cm.
Date	5. 5. 34	5. 5. 34	5. 5. 34	5. 5. 34
Distance from original lake edge (cm.) ...	7·5	17·5	17·5	2·5
Time covered (days) ...	10	4	4	10
Type of environment ...	Long grass	Long grass	Grass, bushes, leaves, etc.	Grass and dead leaves
Leptophlebia sp.	12	7	4	35
Isopteryx sp.	.	.	1	.
Sigara minutissima	100	1	.	1
Agrion pulchellum	1	.	1	1
Endochironomus sp.	1	.	.	.
Gammarus pulex	1	.	.	2
Asellus meridianus	.	.	.	1
Hydroporus palustris	1	3	.	.
Planaria lugubris	1	.	.	1
Anabolia sp.	.	.	.	1
Corixa sp.	6	.	.	.
Thyas venusta	1	.	.	.
Limnesia Koenekii	13	1	.	.
Total of species	10	4	3	7
Total of individuals	137	12	6	42

Numbers represent the population per 9 sq. dm.

Table 3. *Area* = 9 *sq. dm.*

	July		September		September
Time covered (hours) ...	6		7½		15
Distance above original lake edge (cm.) ...	30		42		45
Depth (cm.)	5		7·5		30
	Bay III	Epley	Bay III	Epley	Epley
Ecdyonurus sp.	1	2	.	.	6
Centroptilum sp.	.	1	.	.	.
Gammarus pulex	2	.	.	.	4
Hydraena gracilis	1	3	.	.	.
Dytiscid larva	1	.	.	.	.
Limnophilius rhombicus	1	.	.	.	.
Endochironomus sp.	1	1	1	.	.
Pupae	.	2	.	.	.
Limnodrilius sp.	.	.	.	.	1
Total of species	6	5	1	0	3
Total of individuals	7	9	1	0	11

level of 7·6 -15·2 cm. in 24 hours, while in a big flood the changes in level may be as much as 30 cm. in 24 hours. In the usual type of flood the fauna can keep pace with the rising water, but in a big flood it is left behind. Table 3 gives collections from the floods of July and September 1932. The curves for these two floods are given in Fig. 2. It is noticeable how, in the September flood, areas covered for the same length of time as those in the July flood were almost devoid of fauna. A collection from 30 cm. (1 ft.) in September shows that the fauna was actually moving on to the flooded area.

The evidence indicates that even when the lake reaches a very high level, certain members of the fauna move right up to the new lake edge. In the flood of October 1934 the lake level was 40·3 m. O.D. *Ecdyonurus* nymphs,

Haliplus larvae and *Gammarus pulex* were collected along the edge of the flood, together with the beetles, *Platambus maculatus* and *Haliplus* sp.

The actual horizontal distance moved varies with the flood. The parts of the shore on which flood movements were investigated were not steep, a rise in lake level of 60 cm. (2 ft.) covering considerable areas. The usual distance traversed by the fauna is approximately $1\frac{1}{2}$–2 m. In big floods members of the fauna may move as much as 4 m. In the September flood of 1932, larval Leptocerids 2 mm. in length were collected. These larvae must have crawled 2·7 or 3 m. In the October flood of 1934 several *Limnaea peregra* were found on the lake edge on Watbarrow Point, a vertical rock face. These Molluscs had moved a vertical distance of about 0·6 m.

4. Factors controlling movement of the fauna.

In a previous section the movement of the fauna under flood conditions was demonstrated, the general conclusion being that given a flood of sufficient duration flooded areas would all become colonised by the movement of the fauna. This extensive colonisation is prevented by the fact that as the water rises it covers areas with a type of substratum very different from that which the fauna normally inhabits.

The influence of the substratum on the movement of the fauna was seen clearly in the flood of May 5th, 1934, when the flood covered the grass at Epley Head. Collections made on grass were compared with collections from trays of stones placed on the grass, where normally no stones would be found. The collections from the grass were made in proximity to the trays of stones. The results are given in Table 4. Table 3 shows clearly how the substratum controls the degree of immigration on to the flooded areas. On the stones there is a marked increase in the numbers of *Ecdyonurus*. Also on the stones there is an increase in the numbers of *Isopteryx* and to a certain extent *Leptophlebia* and *Gammarus pulex*. In the case of *Sigara*, however, the greatest numbers occur on the grass, while on grass and stones the numbers are very low.

Table 4. *Quantitative basis of* 36 *sq. dm. Epley Head, May 25th,* 1934.

Depth (cm.)	12·2		20		20	
Time covered (days) ...	3		5		5	
	Grass	Stone and grass	Grass	Stone and grass	Grass	Stone and grass
Ecdyonurus sp.	1	5	1	13	1	10
Centroptilum sp.	.	.	1	.	.	.
Leptophlebia sp.	2	3	1	4	1	4
Isopteryx sp.	2	8	1	7	2	3
Nemura sp.	.	.	.	1	.	.
Sigara minutissima	6	1	8	1	4	.
Gammarus pulex	.	.	1	1	.	6
Total of species	4	4	6	6	4	4
Total of individuals	11	17	13	27	8	23

In the flood of October 1934 these experiments were repeated under more rigorous conditions (see Table 5). Trays of stones were placed on grass which had been covered for 13 days. The trays were left for 3 days, so that when they were lifted the surrounding grass had been covered for 16 days—over four times as long as the trays. They showed very clearly indeed the preference of *Ecdyonurus* for stones and how the establishment of this animal must be limited by the presence or absence of stones. The presence of stones also had an effect on the other members of the fauna. Despite the fact that the grass had been covered four times as long as the trays, the colonisation of the trays had proceeded so rapidly that the population of the trays of stones exceeded that of the bare grass. Further evidence was obtained from the distribution of *Gammarus pulex*. The population of *Gammarus pulex* on an area of coarse shingle with many dead leaves and covered for 15 days was 81 per 144 sq. dm. On an area of grass with few dead leaves and covered for the same length of time and at the same depth, the population was 25 per 144 sq. dm. Experiments in the laboratory have shown that *Gammarus pulex* favours a substratum of coarse shingle, and feeds on dead leaves. This suggests a reason why *Gammarus pulex* was not common on bare grass. The facts indicate, therefore, that change of substratum is the factor limiting the movement of the fauna over flooded areas.

Other factors considered were temperature and oxygen, but there was no significant differences, in regard to either oxygen or temperature, between the original habitat and the flooded areas.

Table 5. *Epley Head, October* 1934. *Depth* = 10 *cm.*

	Grass 144 sq. dm. Two collections amalgamated	Grass and stones 72 sq. dm.	Grass and stones 72 sq. dm.
Ecdyonurus sp.	2	40	20
Coenis sp.	.	.	1
Centroptilum sp.	3	.	.
Leptophlebia sp.	3	.	.
Nemura sp.	1	.	.
Silo sp.	.	1	7
Glyphotaelius sp.	4	4	3
Leptocerus sp.	.	3	3
Hydroporus palustris	2	.	1
Haliplus larva	.	.	1
Tanypus sp.	.	3	.
Sigara minutissima	1	.	.
Sida crystallina	Common	1	.
Gammarus pulex	25	4	.
Hydracarina	2	.	1
Limnaea peregra	1	.	1
Polycelis nigra	.	1	.
Total of species	11	8	9
Total of individuals	44	57	38
		95	

5. Sensitivity of the fauna to changes in lake level.

An important feature of flood movements is the sensitivity of the fauna to changes in the level of the lake. Changes in level of a few inches are sufficient to bring about a movement of the fauna on to the flooded area. Table 6 gives examples of this sensitivity, and in one case it will be noticed that after 12 hours nine different species have responded to a change of level of 2·5 cm.

Table 6.

Flood	November 1933	March 1934	May 1934
Time covered (hours) ...	16	120	12
Rise in lake level (cm.) ...	5	5	2·5
Area (sq. dm.)	16	72	72
Ecdyonurus sp.	.	.	3
Centroptilum sp.	1	.	.
Coenis sp.	.	1	.
Leptophlebia sp.	.	.	2
Nemura sp.	.	1	.
Isopteryx sp.	1	11	10
Polycentrophus sp.	.	8	1
Stenophylax nigricornis	12	.	1
Sigara minutissima	.	1	4
Elmis sp.	.	.	2
Gyrinus larva	.	2	.
Oligochaeta sp. (?)	.	.	.
Limnodrilius sp.	.	1	.
Haemopsis sp.	.	.	1
Gammarus pulex	12	.	4
Sphercon clupeifer	.	1	.
Total of species	4	9	9
Total of individuals	26	26	28

This effect might be explained on the assumption that floods are associated with rough weather which disturbs the fauna. Flood periods, however, are often calm, and colonisation takes place on sheltered as well as exposed shores: e.g. Table 5 gives examples from collections made under sheltered conditions.

6. Nature of the movements.

When the movements of the fauna over a flooded area are considered more closely, it is seen that the movements take place in two stages. The evidence for this is given in Table 7, which gives three separate collections. In each collection four trays were used, the trays being placed along the shore in a row. After the trays had been covered for the required time by the flood, two of the trays were taken up and their fauna collected. After the desired interval of time the remaining two trays were taken up and their fauna removed. In this way the fauna at approximately the same place in the flooded area could be compared at two different times.

In this table it is noticeable how the fauna of an area covered for 2 days is approximately the same or even less than that of an area covered for a much shorter period. If the initial rate of movement over the flooded area was maintained one would expect a bigger population on the trays that had been

Table 7. *Population per* 144 *sq. dm.*

Depth (cm.)	5	12·5	5	5	2·5	3·5
Time covered (hours)... ...	8	48	19	43	12	36
Date	17. 5. 34	17. 5. 34	17. 5. 34	17. 5. 34	9. 5. 34	9. 5. 34
Ecdyonurus sp.	13	21	12	12	3	3
Leptophlebia sp.	3	.	.	1	2	.
Coenis sp.	1	.	.	.	.	.
Isopteryx sp.	28	8	20	12	10	3
Nemura sp.	1	1	.	.	.	1
Polycentrophus flavomaculatus	.	.	.	.	1	.
Stenophylax nigricornis	2	2	.	.	1	1
Platambus maculatus	3	.	.	1	.	.
Haliplus sp.	.	1	.	.	.	.
Elmis sp.	.	.	.	.	2	.
Sigara minutissima	1	.	1	.	4	.
Chironomid sp.	.	.	.	.	.	1
Haemopsis sp.	.	.	.	.	1	.
Gammarus pulex	3	10	4	.	4	13
Total of species	9	6	4	4	9	6
Total of individuals	57	43	37	27	28	22

Table 8.

Depth (cm.)	3·5	7·5
Time covered (days)	26	28
Distance from original lake edge (cm.)	10½	7½
Quantitative basis (sq. dm.)	144	144
Ecdyonurus sp.	1	4
Centroptilum sp.	1	.
Isopteryx sp.	27	37
Nemura sp.	14	20
Sericostoma personatum	.	1
Stenophylax nigricornis	9	12
Agapetes sp.	2	.
Polycentrophus flavomaculata	1	1
Elmis larva	.	2
Hydraena gracilis	3	1
Gyrinus larva	.	2
Tanypus sp.	1	.
Stichtochironomus sp.	3	1
Endochironomus sp.	1	.
Limnodrilius sp.	4	3
Haemopsis sanguisuga	1	.
Herpobdella atomaria	.	1
Gammarus pulex	26	62
Total of species	16	12
Total of individuals	96	145

covered for a longer period. As an explanation for this it is suggested that the members of the fauna which are the first to respond to a flood are those inhabiting the first few inches of the lake. These move over the flooded area, but as the area to be colonised increases with the rising of the flood, the number of animals is not sufficient and the population over the flooded area decreases. The main bulk of the fauna moves more slowly, as can be seen in Table 8, which records the collections from trays which were left down for a long period. It will be seen that the fauna in Table 8 approximates closely to the normal littoral fauna (Moon, 1934). Evidence of a similar nature was collected in the floods of July and September 1932.

The decrease in the amount of movement of the fauna over the flooded area may be due to shortage of food. Normally about 14 days would have to elapse before there was even a sparse algal growth on which the fauna could feed. It will be seen from Table 7 *Isopteryx* and *Ecdyonurus* sp. decrease in numbers, while *Gammarus pulex* increases. *Isopteryx* is a carnivore (Rousseau, 1921) and *Ecdyonurus* an algal feeder (Moon, 1934), and obviously a recently flooded area will contain very little food for either. *Gammarus pulex* would find sufficient nourishment in the dead leaves and debris on the flooded area. This probably explains the fact that *Gammarus pulex* does not decrease in numbers after the initial colonisation of the flooded area.

The later movement of the main bulk of the fauna over the flooded area probably represents the establishment of normal food relations.

7. The retreat of the fauna.

Just as the fauna moves up with the rising water, so it retreats as the flood subsides. There is no indication that members of the fauna are left behind. Only in small land-locked puddles are animals occasionally cut off.

The movement of the aquatic fauna in relation to change of level in the lake is in contrast to the terrestrial fauna. During collections over flooded areas drowned terrestrial animals are common, for example Araneidae, Coleoptera (larvae), Myriapoda and Lumbricids.

In some cases the terrestrial fauna shows a considerable capacity for enduring prolonged submersion. In the flood of January 1934 living Orthoptera, and Coleopterous larvae were found on land submerged for 36 hours. In another collection Lumbricids were found alive on land submerged for 24 days.

8. Causes of the movement.

The evidence regarding flood movements shows that any rise in lake level, however small, is followed by a movement of the fauna over the flooded area. The members of the fauna first to respond to the flood are those animals in the first few inches of the lake. The main bulk of the fauna moves up more slowly. Both movements are ultimately checked by the substratum becoming gradually more terrestrial in nature, the stones and shingle of the shore being replaced by bushes, trees and grass.

With regard to the actual causes of these movements, several possibilities can be considered. Trays covered with stones and shingle from which the fauna had been removed were placed at the required depths in the littoral region. It was found that these trays were rapidly recolonised by the fauna (see Table 9). In one case it will be seen that in 8 hours animals had moved on to a tray. These results have been repeatedly confirmed, and it was found that larger trays left on the lake bottom for 4 or 5 weeks collected a population approximating closely to the normal littoral fauna (Moon, 1935). The evidence

shows that the whole fauna is in a state of movement irrespective of whether or not there is a flood.

Table 9. *Area of tray* = 9 *sq. dm.*

Locality	Epley Head	Bay IV	Epley Head	Bay III	Bay III
Depth (cm.)	60	30	30	60	120
Time covered (hours) ...	24	8	11	24	24
Date	9. 9. 32	22. 8. 32	22. 8. 32	8. 9. 32	8. 9. 32
Ecdyonurus sp.	7	2	11	.	.
Coenis sp.	1	.	.	.	.
Centroptilum sp.	1	.	.	.	.
Nemura sp.	1	.	.	.	.
Lepidostoma hirtum	.	.	.	5	12
Limnophilius politus	.	.	.	5	4
Stenophylax sp.	.	.	.	1	1
Mystacides nigra	.	.	.	.	1
Leptocerus aterrimus	6	.	.	.	.
Agapetes sp.	1	.	.	.	.
Sericostoma personatum	.	.	.	1	.
Sigara minutissima	.	.	.	1	.
Chironomidae sp.	.	2	1	.	.
Limnaea peregra	.	.	.	.	1
Ancylus fluviatilis	.	2	1	.	.
Gammarus pulex	1	.	.	1	4
Planaria lugubris	.	.	.	3	1
Polycelis nigra	.	.	1	4	1
Hygrobates naicus	1	.	2	.	.
Total of species	8	3	5	21	25
Total of individuals	19	6	16	8	8

Table 10.

Species	Date of flood	Depth cm.	Distance above normal lake edge cm.	Time covered by flood	Population per 36 sq. dm.	Date of emergence (approx.)
Isopteryx sp.	29. 3. 34	2·5	5	24 days	8	15. 5. 34
	17. 5. 34	5	2·5	8 hours	14	
Ecdyonurus sp.	29. 4. 34	5	12·5	6 days	3	1. 6. 34
	23. 5. 34	20·5	60	4 days	13	
Leptophlebia sp.	25. 1. 34	15·5	23	21 days	10	20. 5. 34
	20. 5. 34	15·5	7·5	4 days	74	

There is also evidence which suggests that the actual physiological state of the animals themselves may be important. It was observed that those insect nymphs which were near the point of emergence were most conspicuous on flooded areas (see Table 10). When the figures given in this table are considered, together with the length of time that particular areas were available for colonisation, it will be seen that movement on to the flooded areas is undoubtedly more rapid just before emergence than at an earlier date.

It is also significant that at the period of emergence the greatest number of mature nymphs are to be found at the edge of the lake in about 2·5 cm. of water.

There are two possibilities, either insects at the point of emergence are more active than normally, or else they respond to a taxis which sends them into shallower water, and if the lake is in flood they are compelled to move

on to the flooded area. On the other hand, the fact that insects not near their emergence move into flooded areas, and that flood movements take place in those months when no adults are appearing, suggests that the tendency for colonising unoccupied places on the lake shore is inherent at all stages.

Evidence concerning this last point was obtained in the October flood of 1934. In this flood young stages of *Coenis* (2·0 mm.), *Ecdyonurus* (1·5–4·0 mm.), *Leptophlebia* sp. (2·0–3·0 mm.), and *Limnophilus rhombicus* (2·0 mm.) were found $2\frac{1}{2}$ m. away from the original lake edge. Associated with these young forms were a number of mature forms which actually emerged while the collections were being sorted. This was conclusive proof that both mature and immature forms had moved on to the flooded areas, and that the movement of insect nymphs cannot be entirely explained by a physiological change associated with maturity.

One is forced to the conclusion that although the physiological state of an insect larva or nymph may have an influence in determining the extent to which movement will take place, the tendency for movement is present all the time. The fact that all active members of the fauna besides insects show the same movement is proof that the tendency for movement on to flooded areas is common to the whole fauna. Flood movements are only special manifestations of the movements which are always taking place in the littoral region.

We see therefore that movements of the littoral fauna are always taking place, and that the colonisation of a flooded area is the outcome of this random movement. The evidence suggests that the degree of colonisation of flooded areas depends upon three factors:

(1) Rate of movement of the animals themselves.
(2) Food supply and suitability of the substratum.
(3) Physiological state of the animals themselves.

These three factors are all interrelated. Even if approaching maturity has increased the activity of the nymphs, the food supply may be insufficient to support those which move on to the flooded area. Or again, when the lake level alters rapidly the fauna may not be able to move sufficiently rapidly to colonise the bare areas, even though the substratum is suitable.

9. Summary.

1. During the course of an investigation of the littoral region of Windermere it was found that the fauna was in a continual state of movement. Artificially depopulated areas were rapidly recolonised. These movements were clearly seen in periods of flood during which considerable numbers of the aquatic fauna moved on to the inundated areas.

2. Quantitative evidence regarding these movements was obtained by means of a special scoop and a system of collections from trays, which were covered with stones and shingle in imitation of the substratum.

3. Records were kept of lake levels and the time and depth of each collection. In this way it was possible to estimate how long a particular area had been covered by the flood.

4. The more active members of the fauna, e.g. *Ecdyonurus* sp., *Isopteryx* sp. and *Gammarus pulex*, move on to the flooded area exceedingly quickly. An area covered by the flood for only 8 hours can usually be expected to contain a small fauna.

5. The fauna is extremely sensitive to changes in level of the lake. A rise in level of only 2·5 cm. is sufficient to bring about a movement of the fauna.

6. Given sufficient time the littoral fauna would ultimately colonise a flooded area completely. The main check on extensive colonisation is the change of substratum associated with the terrestrial character of the flooded area. For example, experiments showed that absence of stones checks the movement of *Ecdyonurus* onto grass.

7. The evidence suggests that it is food shortage which checks the initial movement of the fauna. Only after the appearance of an algal growth can the main mass of the fauna colonise the inundated area.

8. Flood movements are only a special manifestation of the "random movements" which are always taking place and are characteristic of the whole fauna. Under certain circumstances, however, these movements may be modified by the actual physiological state of the animals themselves.

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AN EXPERIMENT ON THE POWERS OF SURVIVAL OF ANIMALS AND PLANTS FROM A POOL ABOVE HIGH-WATER MARK

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Whilst investigating the life history and ecology of the Harpacticid Copepod *Tigriopus fulvus* (Fischer) (**1**), an experiment was made to test its resistance to unfavourable conditions, and as many of the incidental results are of interest it is perhaps worth while to give a complete account of the experiment. A jar half-filled with water from a pool above high-water mark at Port St Mary, Isle of Man, and containing numerous *Tigriopus fulvus*, was sealed and kept for two years at the University College of Hull. No special nutrient material had been added. Many of the forms were too small to be seen without a microscope and so their progress could not be followed. The *Tigriopus* thrived well and bred for almost a year. During this time the sides of the jar became coated with a thin green film and some *Enteromorpha* was seen to be growing; all traces of green, however, gradually disappeared, leaving only a colourless scum. Observations made through the glass clear enough for the purpose revealed that some *Tigriopus fulvus* were still active, while large numbers of others apparently were resting. These retained their orange colour and could readily be distinguished from the dead. A few remained active for as long as 18 months, after which no sign of activity could be seen.

After two years the jar was opened, the contents stirred (but nothing added), and then left uncovered near an open window. The *p*H was 8·7, and there was very little trace of bacterial action. Searches through samples taken from the jar revealed a few small orange *Tigriopus*, apparently dead, many cast skins of all stages and many disintegrating bodies. Empty half-shells of Ostracods (*Cythere lutea* O.F.M.) were present. Nothing else of interest was seen, the rest seeming to consist of a scum.

A week later signs of green appeared and young *Enteromorpha* filaments became established. The green scum consisted of filaments of the blue-green Algae *Phormidium tenue*, *Nostoc*, and a gelatinous mass of Coccogonales, probably either *Gleocapsa* or *Pleurocapsa*. All the latter forms would have developed from resting stages, and the *Enteromorpha* from akinetes. The water was teeming with very small Ciliates, and some Flagellates were present. A few small *Tigriopus* were found to be alive and active: they were mainly late copepodids and adults, all stunted (about half to three-quarters of the normal length at that stage). Casts of other stages, similarly stunted, were also found.

Three weeks later more active and more abundant *Tigriopus* were found, though still of a stunted nature, and numerous very active *Cythere lutea* were seen crawling amongst the debris. These, too, were smaller than the normal size, and some very small cast shells were found. Another Harpacticid, *Amphiascus minutus* (Claus), was found, very active and almost natural size, but not so numerous as *Tigriopus*, from which it could be distinguished at a glance by its lighter colour and the long sensory appendages on the first antennae. That these forms were all well developed excludes any possibility of their having come from resting eggs; their stunted nature, and the presence of stunted casts indicates that some activity had been going on all the time, and that the adult forms are themselves highly resistant to unfavourable conditions and can live in a very limited oxygen supply.

A Turbellarian, *Gunda ulvae*, or a species closely resembling it, was present and active. This stage—a month after opening—seemed to be the climax, for since then the *Enteromorpha* has died down to a great extent and the green of the scum, seven weeks after opening, is not so vivid; the animal life, too, is less abundant and less active.

Summary.

A jar half-full of water from a pool above high-water mark was kept sealed until all plant and animal life was apparently dead or dormant. After two years the jar was opened, and within a month a carpet of blue-green algae with some *Enteromorpha* was visible. Active *Tigriopus fulvus*, *Amphiascus minutus* and *Cythere lutea* were found, though stunted in size. Evidence shows that these had not developed from resting eggs but must have been slightly active throughout. A Turbellarian, numerous Ciliates, and some Flagellates were also present. Little bacterial action had taken place and the *p*H was high. After seven weeks activity was much diminished.

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THE ECOLOGY OF BARDSEY ISLAND: TOPOGRAPHY AND TYPES OF ENVIRONMENT

By F. LOXHAM KIDD, K. A. PYEFINCH and P. M. BUTLER.

(*With Plates* 7 *and* 8 *and* 1 *Map in the Text.*)

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1. Introduction.

The account given below is that of a visit paid to Bardsey Island in July and August 1933, in order to make an outline ecological survey as a preliminary to a more detailed investigation later. The latter is planned to last for a period of years, and thus we hope to attempt not only a description of the ecology, but also to trace the more important changes in an island population over a number of years.

Bardsey Island was chosen as the site of this survey for several reasons—it is moderately accessible and thus can be visited frequently, it is of a reasonable size, it offers a wide variety of habitats, it has been inhabited for a considerable time, and thus the ecological results obtained will give a better idea of normal conditions than those of a small uninhabited islet, and, though only a short distance from the mainland, the nature and speed of the currents in the Sound are such as to preclude much direct immigration across it.

Several travellers of the eighteenth century mention the island, the best account being by Sir D. Pennant (**14**), who visited it in 1778. He landed at the old landing place on the west side of the isthmus. The island had about eighty people on it. He mentions the fertility of the soil and says that the upland served as pasturage, supporting some sheep and numerous rabbits. Bingley (**3**) in 1798 and Evans (**10**) in 1800 added little to this account, most of their material being taken directly from Pennant. Evans noted the absence

of reptiles except "water lizards"—by which it is presumed he means the newt. He also says that puffins rested on the island, but perhaps this is a mistake for shearwater, since the two birds have often been confused. At present the nearest resting place for puffins is Puffin Island, and it seems doubtful if they ever occurred on Bardsey.

As well as these early descriptive visits, there are records of frequent visits by ornithologists. As the birds of the island have been dealt with at length by Coward (**8**), Aplin (**1**), Johnson and others, it is not intended to include a bird census in the present survey. So far as we have been able to trace, the only other visit by a naturalist of which a published record exists (**16**) is that of Scott in 1902. He visited the island for a week, and whilst there made a collection of the fresh-water animals.

2. The history of the island.

Nothing is known of the island in prehistoric times, but from about A.D. 500–1583 it played a considerable part in the ecclesiastical history of Wales. The first records show that a band of hermits, the Caelebes, settled on the island about A.D. 500 and that about 520 St Dubricius retired there, later to be followed by St Daniel and others. The place gradually became a centre for pilgrimage from all parts and the monastery, which succeeded the band of hermits, became rich and powerful.

The origin of the name seems uncertain. Pliny (**15**) mentions an island, Andros, which Camden (**7**) believed to be Bardsey, from the Welsh "Ader"—a bird, a point which the English used later in calling it Berdsey—the island of birds. The modern Welsh name "Ynys Enlli" means the "Isle of the Current", a very suitable description, but Camden thought that it was derived from "Ynys Henli"—from "Henli", a hermit who lived there. Anyhow, the island has been inhabited for at least 1400 years, and the influence of man must have been profound. For instance, from documentary evidence and an analysis of the present flora, it seems that there was a considerable number of trees on the island in the early days. The effect of grazing animals and the need for fuel must soon have wiped them out until a few willows, a plum tree, an elderberry, a stunted sycamore, and a minute hawthorn are all that remain to-day. Many of the present animals and plants must have been introduced during this period of occupation.

3. Physiography.

The island lies in the north of Cardigan Bay, about 1¼ miles from the extreme point of the Lleyn Peninsula and separated from it by the dangerous Bardsey Sound. It is reached by boat from Aberdaron, a little fishing village on the south side of Lleyn. The crossing is seldom pleasant, and often impossible. Rounding the promontory of Braich-y-Pwll, the boat meets the full force of the sea, and from there onwards great care has to be exercised. In

Phot. 2. Bardsey Island from Braich-y-Pwll.

Phot. 3. The landing place at low tide, showing dense growth of seaweed.

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winter, the island may be isolated for several weeks at a time, and spells of a week are not uncommon even in summer. The currents run at 6 knots and at the turn of the tide even more in the Sound, and a rather circuitous crossing of about 6 miles has to be taken.

From the mainland the island appears much more forbidding than it actually is, as the highest land is on the east and this hides the gently sloping western part from view. Bardsey consists of two parts. The larger, *northern portion*, roughly rectangular in shape and having a mountain rising up to 550 ft. on its eastern side, whilst a gently sloping plain forms its western side. The smaller, lower *southern portion*, is joined to the former by a narrow isthmus across which in winter waves sometimes sweep. It is on the western side of the northern part that the *farms* are situated. In the past the cultivated land was split up into small holdings, but now it is divided into six farms. Some of the houses are vacant, and in the case of others two have been made into one. The present farmhouses are well built and were constructed in 1876 on or near the sites of older buildings. A typical feature is the strong, high wall round the farmyard, built for the protection of cattle and sheep against the winter storms.

There is only one *road* on the island: it starts from the lighthouse and runs past the landing stage up the centre of the island, as far as the chapel, passing all the farms on its way. There is little surface other than the bare rock, but it serves well enough for the few wheeled vehicles on the island.

The *mountain* is covered with grass, bracken and gorse affording good pasturage for a number of sheep. The *plain*, which has long been noted for its fertility, is for the most part under cultivation in barley, oats, potatoes, turnips, etc. The work is done in rather a desultory fashion, time being of little importance. The men are also fishermen, good catches of mackerel being often taken, whilst the pots catch lobsters of good size. Until recently the abundant supplies of sea-weed were utilised as manure, but nowadays this practice seems to be falling out of use, the crops depending at present on the excess manure put on by the old islanders.

The *climate* of the island is favourable, snow being very rare. The rainfall, judged from the neighbouring stations on the mainland, is at least 36 in. per annum. Strong winds are frequent and mists often hang over the island for days on end. Thunderstorms are exceptional. The *geology* of the island is complex, but two main types of surface occur. These consist of slate—including the whole of the mountain and outcrops at various parts of the lowland, and boulder clay —which, extending over most of the lower land, forms a fertile soil. Various intrusions of diabase, quartzite, limestone and granite occur. Slate outcrops in the boulder clay region are covered with a gorse-bell-heather association, whereas the boulder clay in the immediate neighbourhood bears a regular meadow flora (grasses, clover, buttercups, etc.), the sudden transition being most striking. In places the island shows considerable

ice scratches, so that it seems probable that it must have been completely glaciated. Whether it was separated from the mainland in pre- or post-Glacial times is unknown. On the steep eastern side there are signs of a great landslide, but as to when this occurred we found no evidence. Lastly, there is the interesting problem of what appears to be a raised beach on the isthmus. Matley (in a personal communication) interprets this as the end of a beach, further traces of which occur on Seagull's Island in Aberdaron Bay. The only other possible trace of such a beach on Bardsey is a sandy cliff at a point about half-way along the eastern side of the mountain, but it is just possible that both are storm beaches. Matley (**12**) has carried out an extensive geological survey, so that the reader may be referred to his paper for further details.

For ecological purposes, the major regions of the island are the *Shore*, the *Land* and the *Fresh Water*.

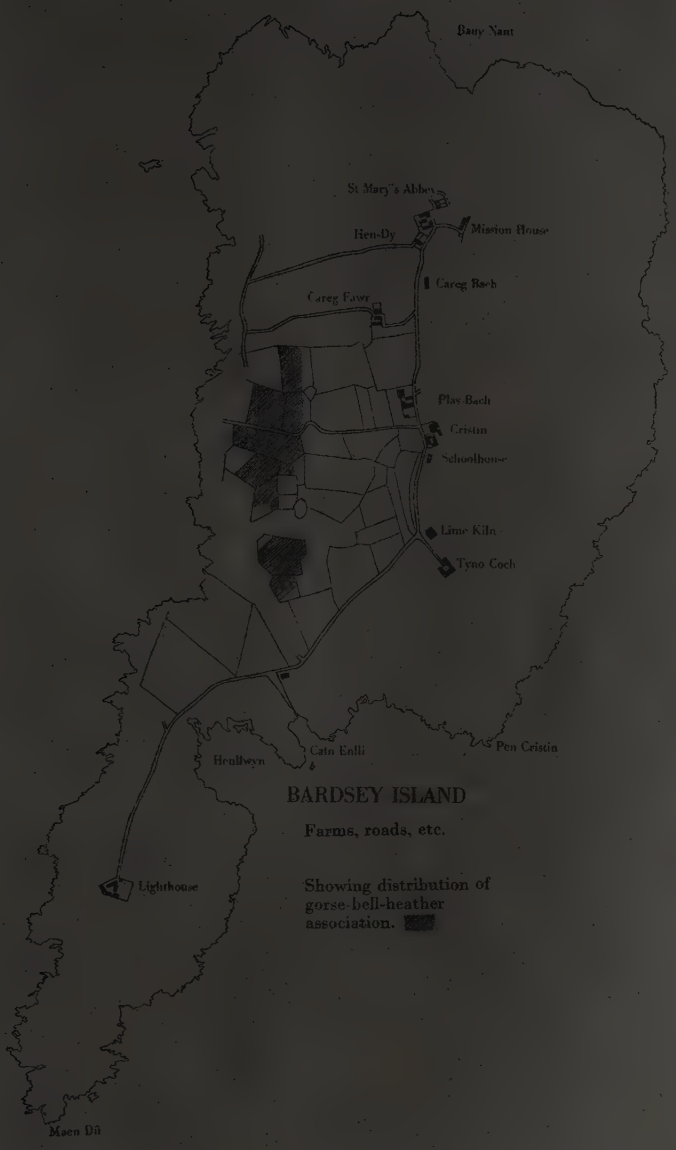
4. Fauna and flora.

(*a*) *The shore.*

The shore may be divided up into *Rocky*, *Shingle* and *Sandy* areas. The relative extent of these may be judged from the map.

Rocks. The largest part of the shore consists of hard slate and diabase, being the base of cliffs which, with the exception of those of the isthmus, have a hard rock surface and fall steeply to the sea for at least 50–100 ft. These great irregular rock masses are scoured by the sea, so that few crevices afford sufficient protection for animal life. In consequence the fauna is scanty: the commonest animals being barnacles (*Chthalamus* and *Balanus*) forming a white strip stretching up to high-water mark around much of the eastern shore, molluscs (*Patella*, *Patina*, *Gibbula*, *Littorina* and *Nucella*) chiefly in and among large masses of sea-weed, and sea-anemones (*Actinia* and *Anemonia*) within the clefts of the rocks. As well as being few in number many of the sedentary animals show by their form the effect of wave action, e.g. the sponges *Halichondria panicea* and *Hymeniacodon sanguinea* and the Tunicate *Botryllus schlosseri* are all found as thin, flat plates deep within the rock crevices. The sea-weeds are both abundant and varied, over 40 species having been found. These range from delicate red ones to the great *Laminaria* fronds which occur in deeper water and are washed up in enormous quantities after storms. In many places coralline algae cover the rocks, their growth being well suited to the rough conditions. In some places there are pools containing green algae and only touched by the highest tides. They offer an environment of extreme type both in regard to temperature and *p*H, the activity of the algae often rendering their surrounding water alkaline. The sole animals in these pools appear to be one or two Crustacea.

Shingle. This is restricted to two small areas, one on the east side of the isthmus between the low boulder-clay cliffs and the hard rocks beginning near low water mark, the other in a sheltered area north of Porth Solfach. The latter



BARDSEY ISLAND

Farms, roads, etc.

Showing distribution of gorse-bell-heather association.

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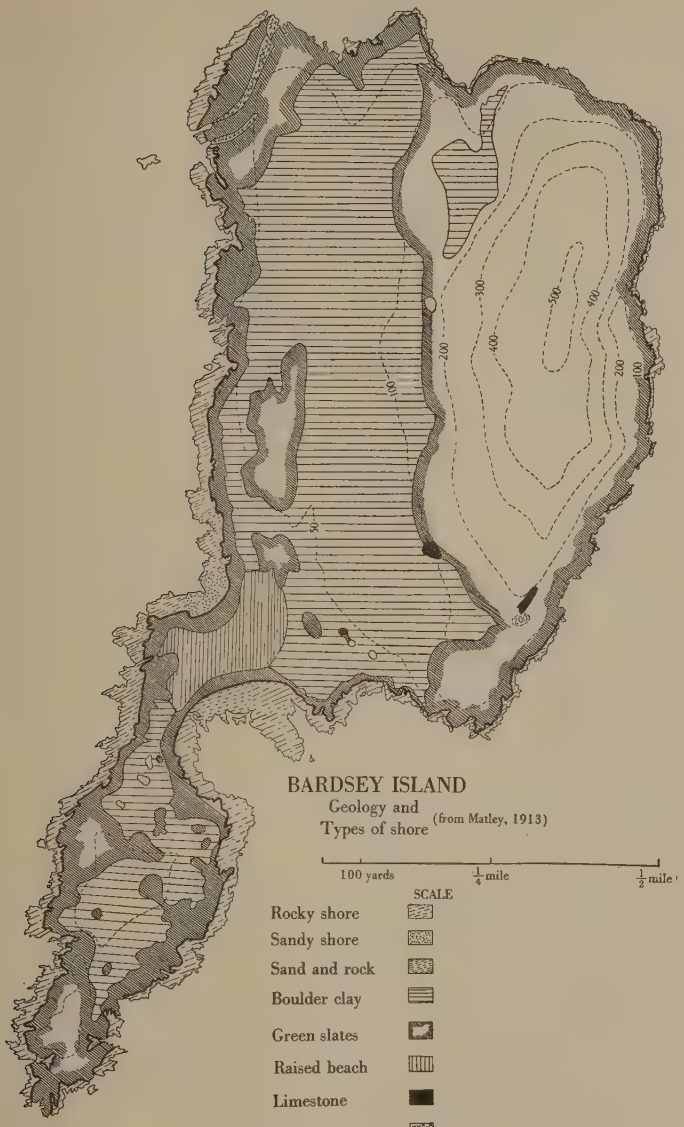
RAMSEY ISLAND
Farms, roads, etc.
showing distribution of
gorse bell-heather
association


BARDSEY ISLAND
Geology and
Types of shore
(from Matley, 1913)
100 yards
¼ mile
½ mile
SCALE
Rocky shore
Sandy shore
Sand and rock
Boulder clay
Green slates
Raised beach
Limestone
Granite
High water mark

Map 1.

is the only place with a soft substratum and stones large enough to afford shelter. Only here occur such forms as polychaetes, nemertines and the echinoderms, *Asterina gibbosa*, *Amphiuma squamata* and *Ophiothrix fragilis* though not in any abundance. The portion on the east side of the isthmus is a more extreme habitat only covered by highest spring tides and so almost completely barren.

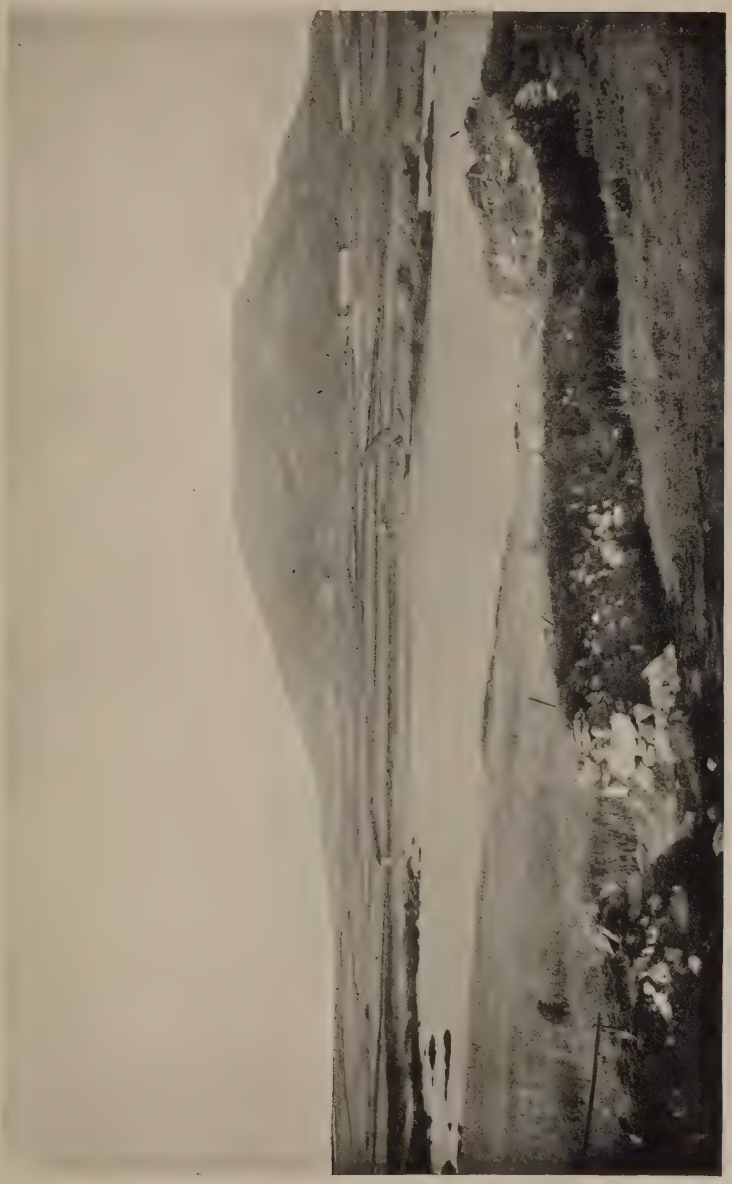
Sand. An area of sand about 100 yards long occurs within the bay of Porth Solfach. It stretches back from low-water mark to the low boulder-clay cliffs. Just below low-water mark is a belt of sea-weed, extending several yards into the sea. The whole bay is very sheltered, and in the absence of wave action this sea-weed area is practically stagnant. The sea-weed belt swarms with the Isopods, *Idotea baltica* and *Dynamene bidentata*, and the fronds themselves are covered with *Aglaeophenia tubulifera*, *Obelia geniculata* and *Sertularia gracilis*, but the perisarcs of many of these Hydrozoan colonies were empty. The whole area is foul-smelling, that part which is permanently moist being black: even the drier bleached part is black a few inches below the surface. It is seldom that such an area can be shown to be entirely free from the effect of sewage, and so this shore is of particular interest. The suggestions of Bruce (**6**) arising out of his work at Port Erin, and the investigations of others on the Black Sea deposits, fit in well with the facts to be noted in the area. The depth at which the black layer begins is the equilibrium point between the supply of O_2 and S, the latter depending on bacterial actions on inorganic sulphates in the presence of carbon. Decaying algae can certainly supply sufficient organic matter, as after rough weather the beach is thick with *Laminaria* and other algae. These may well supply the inorganic sulphates, since their ethereal sulphate content is known to be high. The hydrogen sulphide eventually generated reacts in part within the iron in the sand, forming iron sulphides, the remainder escaping into the air. A theoretical scheme is:

$$CaSO_4 + 2C \xrightarrow[\text{Bacteria}]{} CaS + 2CO_2$$
$$CaS + 2H_2O + 2CO_2 \longrightarrow Ca(HCO_3)_2 + H_2S$$
$$H_2S + Fe(OH)_3 \text{ etc.} \longrightarrow FeS + Fe_2S_3.$$

The sand is fine and therefore aeration is difficult, and as there is a large supply of sea-weed the conditions on this part are ideal for the formation of such a black layer.

(*b*) *The land.*

The boulder-clay lowland is cultivated, while the slate on both upland and lowland is uncultivated. The upland shows a transition from gorse (*Ulex*) as the dominant plant, through heather (*Calluna*) to grass and lichens at the top of the mountain, with bracken (*Pteris*) extending all the way and at times replacing each of these dominants. The flora is affected by the sheep and rabbits which occur all over the uncultivated area. The flora of the lowland,



Phot. 1. View from lighthouse, looking North, showing mountain, farms and shingle beach.

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as previously mentioned, varies with the underlying rock, for apart from differences in the physical and chemical make-up, the depth of soil is much less over the slate than in the boulder clay. The gorse, which in places covers the ground, appears to be spreading. It offers an ideal habitat for web-spinners, and the garden spider, *Araneus diadematus*, is abundant, particularly in the lowland. The bushes also afford shelter for various wolf spiders, *Lycosa monticola* being the commonest.

Several marshy areas occur on the boulder clay, the largest being in the central part of the plain. The vegetation here is luxuriant and there is a correspondingly rich fauna. These comparatively small areas support some 40 species of plants, horsetails (*Equisetum limosum*), the marsh marigold (*Caltha*), watercress (*Nasturtium*), yellow flag (*Iris*), water mint (*Mentha*), water forget-me-nots (*Myosotis*), willow herb (*Epilobium*) and a meadowsweet (*Spiraea*) being the commonest. A few animals, such as the spider *Pirata piratica*, are confined to these areas.

There is some uncultivated land, covered by heather, at the north and south ends of the island, but as yet no examination of its special associations has been made.

Finally, before leaving the land habitats, special mention must be made of the various banks, walls and caves of the island. The *walls* fall into a graded series beginning with strongly cemented ones and passing through looser structures with an increasing content of earth to stages almost indistinguishable from purely earthen banks. Disruption of the wall gives a wider variety of habitats to both animals and plants. The first stage walls have lichens and mosses on them and a fauna consisting of mites (*Gamasus marginatus*) and occasional spiders (*Segestria senoculata*, *Harpactes hombergii* and *Hophocarhilum nemorale*), evidently feeding on visiting winged insects. At an early stage *Holomachilis* sp. becomes common, and then gradually the animals and plants increase in both numbers and variety.

The earthen *banks* are ancient and appear to have served as the original boundaries of the fields. In the case of the uncultivated land they offer, as Shelford (**17**) points out, an undisturbed habitat and therefore enable plants which are not so well adapted as ephemerals to live at least near, if not actually on, cultivated land. Many of the banks are kept moist by water in ditches at their base, but some near the western edge of the island are dry. So hot in the sunlight were these latter that it is little wonder that the sole living creatures to be found on them are a few red mites. It is hoped that the succession of the flora and fauna will be worked out in greater detail later.

The *caves* are four in number, two on the eastern and two on the western side of the mountain. The two western ones are small and offer little of interest. Of the two caves on the east side the larger is one at the base of the cliffs about a quarter of a mile from Pen Cristin. This cave appears to have been formed by a great landslide at some distant time. The entrance from the land

is through a narrow chink in the rocks. This leads into a cave some 15 ft. square which opens into the large main cave, most of whose floor is covered by 20 ft. of water, as there is an opening below low-water mark. It is through here that seals enter to rest on the rocks. The main part of the cave is about 60 ft. long and 30 ft. wide. On the roof are numerous individuals belonging to the species *Meta menardii*, found only in very damp places. They offer an interesting problem in distribution and also in the nutrition, for the food resources of the cave appear very limited; a small Isopod, *Ligia oceanica*, was the only animal seen caught in any of the webs. In the other cave on this side higher up the mountain a number of spiders, mites and beetles were found. The most interesting was a unicolorous female of the spider *Nesticus cellulanus*. This is an extremely rare variety.

(c) *The fresh water.*

The fresh water is scattered but in normal times is quite abundant. During our stay it was greatly reduced owing to the drought, but a number of permanent springs, used for drinking water, occur on the mountain. In wet weather a few streams run down to the plain, ending in quite large pools which serve as drinking places for the sheep and cattle. These lowland ponds have muddy bottoms: their surface is covered with duckweed, *Lemna minor*. As far as investigation has gone they appear to have a wide variety of inhabitants. In some, the planarian *Polycelis nigra* occurs in strikingly large numbers, whilst in one near the lighthouse the Isopod *Asellus meridianus* was found. This form is interesting in its sporadic distribution, which Tattersall (**18**) thinks may be connected with the geological formation of the ponds where it occurs. This particular pond is near the coast, and in wet weather a little stream runs from it down the cliff face. All that remained of this stream was a series of small pools which showed a gradation from completely fresh water at the top to completely salt water at the base of the cliff 50 ft. below. The eels (*Anguilla anguilla*), which are quite common in the main pond, apparently come up this steep gulley from the sea. They all died when the pond dried up, evidently so overcome by the foul mud as not to be able to crawl away. One large pond at the north end of the island had dried up, even before we arrived in early July. This too was said to have had eels in it.

Much of the fresh water is in small, shallow ponds, which, in the absence of trees or tall surrounding vegetation, are very exposed, causing them to reach a high temperature in the summer. Only one spring had a temperature below 13° C. This one was at the base of the cliffs on the east side, about 15 ft. above high-water mark, and was protected from the sun by overhanging rocks. It was here that the interesting planarian, *Planaria alpina*, was found. This species is usually regarded as an Ice Age relict, and so to find it in this position was rather surprising, for judging from the raised beach it seems that the place has risen at least 20 ft., and therefore at the time of glaciation it

was probably below sea-level. *P. alpina* must therefore have managed to migrate to this spot from higher up the mountain or else have been carried to the place from some other part of the island or mainland. The possibility of the reintroduction of this form seems rather unlikely, since it cannot withstand a temperature much above 12° C., nor any desiccation. Even its cocoons offer little possibility of carriage by birds, both from their sensitivity and the inaccessibility of their normal resting places at the bottom of streams. It is just possible that in some cases *P. alpina* managed to survive in underground water, and this might have been the case on Bardsey. *Asellus meridianus* is a form which is often associated with underground water, though one hardly dares to suggest that this, too, previously existed in such a habitat on the island.

5. Origin of the fauna.

It is not proposed to publish a complete faunal list here, as any list published would be palpably incomplete. Such lists will be published as each habitat is explored in detail. There are certain striking features of the fauna, however, which may be included in this general account. The present fauna must all have reached the island since the Ice Age, for even if the island were not separated before this, it would have been at the latest immediately afterwards, and at this time both it and the mainland would have been rendered desolate by the action of the ice.

The mammals are surprisingly few. The only species found were the shrew (*Sorex araneus castaneus*), the field mouse (*Apodemus sylvaticus sylvaticus*), the house mouse (*Mus musculus*) and the rabbit (*Oryctolagus cuniculus*). Rabbits are common all over the island, but are most numerous on the eastern side of the mountain, on the western edge of the lowland towards the seacoasts, and in a small area near the south-west part of the island. Some are wild, but some are the offspring of domesticated rabbits, liberated in 1925 when the old inhabitants left the island. They are increasing rapidly, and threaten to become a serious menace unless kept in check. An interesting detail is the appearance of a pure white form, three or four specimens of which were seen on the western side of the mountain.

The field mouse and the house mouse are the same as those of the mainland, but the shrew shows slight, but constant, differences from the mainland form. These are: (*a*) darker coloration, (*b*) slightly shorter tail, (*c*) smaller skull, (*d*) darker enamel on the incisors. Miller (**13**) records one specimen of *Sorex araneus castaneus* from Bardsey. The skull measurements he gives differ much more than those of the present series from the mainland forms, and he thus regards the Bardsey shrew as a distinct race. This evidence cannot be regarded as entirely satisfactory, as only one specimen was used.

There are several mammals common on the Lleyn Peninsula but which, though suitable habitats appear to exist, are absent from Bardsey. Examples are: the brown rat (*Rattus norvegicus*), the field vole (*Microtus agrestis*), the

hedgehog (*Erinaceus europaeus*)—though one skin was picked up on the shingle below Y. Cafn, it had obviously been washed ashore—and the mole (*Talpa europaea*).

The island receives many BIRDS other than the normal residents, for a branch of the main northern migration route passes over it, and so exhausted members of the migrating flocks often land. These may be of importance as a means of transport of animals and plants. The REPTILES are represented only by the slow-worm (*Anguis fragilis*), the "sheep snake" of the inhabitants, which occurs among the stones of the older walls and in the cultivated fields. No AMPHIBIA were found, though Coward (**8**) records the presence of a newt, thus confirming the earlier statement of Evans (**10**) that "water lizards" were found. No frogs occur, and there is a curious tradition that any frogs brought to the island at once die when placed in contact with the soil. Only one fresh-water FISH, the eel (*Anguilla anguilla*) was found.

In the INSECTS, the most characteristic features were the small number of *butterflies and moths* (Lepidoptera), and the large number of ants. Only 41 species of Lepidoptera were collected during the whole of our stay. The lighthouse-keepers also stated that few Lepidoptera were collected at the lantern as compared with other stations. The cause of this may be the frequent high winds. The *ants*, comprising 6 species, are present in enormous numbers, parts of the mountain and many of the earthen banks being riddled with their nests. They appear to be important in the distribution of the gorse (*Ulex*). This is spreading rapidly, and in many cases the bushes are found to be developing either on the ant hills or on the paths taken by the ants. This point will be more fully investigated later, and it is hoped that a plot of the gorse bushes together with the smaller bushes round may yield further valuable information about the laws of territory among ants (**9**).

The *beetles* (*Coleoptera*) were also collected as extensively as possible, and the results suggest an interesting problem in geographical distribution. 82 species were collected. Table I gives the species in common between Bardsey and other islands of the west coast.

The exact cause of the difference in the Coleopterous fauna of Skomer and that of the other three islands is not easy to see, but an important factor must be the effect of habitation and cultivation, as Skomer, alone of the quartet, is not cultivated or inhabited.

46 species of *spiders* and 3 species of *Phalangid* were collected, an account of which has already appeared (Bristowe (**5**)). Individual species do not call for special mention, the most interesting form, *Meta menardii*, has already been mentioned. *Pholeus phalangioides*, a spider spread by man, was not found, although conditions of temperature seemed to be suitable. It is interesting to note in passing the important effect of wind as an agent of dispersal of spiders. Of the 8 British species which Bristowe (**4**) deems the best aeronauts, 6 occur on the island.

Table 1. *Comparison of the Coleoptera of Bardsey with those of other islands.*

	Scilly Isles	Lundy	Isle of Man	Skomer
Adephaga:				
Notiophilus substriatus Wat.	–	+	+	–
Clivina fossor L.	–	.	+	–
Ophonus pubescens Mull.	+	+	–	–
Harpalus aeneus F.	+	+	+	–
H. rubripes Dufts.	+	+	–	–
Pterostichus madidus F.	–	+	+	+
P. vulgaris L.	–	+	+	–
P. ignita F.	+	+	–	–
P. strenuus Pz.	+	+	+	–
P. vernalis Pz.	+	–	–	–
Calathus fuscipes Goez.	+	+	–	–
Taphria nivalis Pz.	–	–	+	–
Agonum mulleri Hbst.	+	–	–	–
A. ruficornis Goez.	+	+	–	–
Laccophilus minutus L.	+	+	+	–
Hydroporus palustris L.	–	+	+	–
Agabus bipustulatus L.	+	+	+	+
Palpicornia:				
Hydrobius fuscipes L.	+	+	+	–
Laccobius alutaceus Thoms.	.	.	.	.
Anacaena limbata F.	+	+	+	–
Helophorus brevipalpis Bed.	–	–	+	–
Sphaeridium quadrimaculatum Marsh.	+	–	–	–
Cercyon melanocephalus L.	+	+	+	–
C. haemorrhoidalis F.	+	+	+	–
C. pygmaeus Il.	+	+	+	–
Brachelytra:				
Alochara bipustulata L.	+	+	–	–
Exaleochara morion Gr.	+	–	–	–
Atheta sordidula Er.	–	+	–	–
A. fungi Gr.	+	–	–	–
A. clientula Er.	+	–	–	–
A. zosterae Th.	+	+	–	–
A. longicornis Gr.	+	+	–	–
Amischa analis Gr.	+	+	–	–
Autalia rivularia Gr.	+	–	+	–
Cardiola obscura Gr.	+	–	–	–
Tachyporus solutus Er.	+	+	+	–
T. pusillus Gr.	+	+	+	–
Conosomus lividus Er.	+	–	+	–
Tachinus rufipes Deg.	+	+	–	–
Philonthus albipes Gr.	–	+	–	–
Cafius xantholinus Deg.	+	+	+	+
Xantholinus tricolor F.	+	–	–	–
Staphylinus olens Mull.	+	+	–	–
Stenus nigritulus Gyll.	–	–	–	–
Oxytelus complanatus Er.	+	+	–	–
O. laqueatus Marsh.	–	–	–	–
O. tetracarinatus Block.	+	+	+	–
Platystethus arenarius Fourc.	–	–	+	–
Micralymma marinum Stroem.	.	.	.	.
Megarthrus depressus Payk.	–	+	+	–
Clavicornia:				
Ptenidium pusillum Gyll.	+	+	–	–
Ptomaphagus subvillosus Goez.	.	.	.	.
Meligethes aeneus F.	+	+	+	–
M. picipes Sturm.	+	–	+	–
Enicmus minutus L.	+	+	+	–
Atomaria pusilla Payk.	+	–	+	–
Typhaea stercorea L.	+	+	–	–

Table I (*cont.*).

	Scilly Isles	Lundy	Isle of Man	Skomer
Lamellicornia:				
Aphodius fimetarius L.	+	+	+	−
A. rufipes L.	+	+	+	−
Geotrupes spiniger Marsh.	+	−	+	−
G. stercorosus Scrib.	+	+	+	+
Serricornia:				
Corymbites aeneus L.	.	.	.	.
Rhagonycha fulva Scop.	−	−	+	−
Phytophaga:				
Phaedon cochleariae F.	−	+	−	−
Prasocuris phelandrii L.	+	−	−	−
Longitarsus jacobaeae Wat.	+	+	+	−
L. luridus Scop.	−	+	+	−
Crepidodera ferruginea Scop.	+	+	+	−
Heteromera:				
Blaps mucronata Latr.	+	−	+	−
Rhynchophora:				
Apion nigritarse Kby.	−	+	+	−
A. carduorum Kby.	+	+	+	−
Otiorrhynchus sulcatus F.	+	+	+	−
O. rugifrons Gyll.	+	+	+	−
Strophosomus retusus Marsh.	+	+	+	−
Sitona flavescens Marsh.	+	+	+	−
S. hispidulus F.	+	+	+	−
S. lineata L.	+	−	+	−
Ceuthorrhynchus assimilis Payk.	−	+	+	−
C. pollinarius Forst.	+	+	+	−

Islands	Species in common
Bardsey—Scilly Isles	57
Bardsey—Lundy	52
Bardsey—Skomer	4
Total list	79

A start has been made on the statistical investigation of the Gastropod, *Cochlicella acuta*. This occurs in moderate quantity on the island, principally in dry, sandy places a little way inland. Many of our specimens showed insular melanism, the significance of which has been discussed by Aubertin, Ellis and Robson (**2**), but of which the true cause is as yet unknown.

6. Acknowledgments.

We wish to acknowledge the kindness of the Trustees of the Hon. F. G. Wynn for allowing us to work on the island, Mr C. A. Matley for a geological map, the British Museum (Natural History) for help in identification, and Prof. J. Stanley Gardiner for constant help and interest.

7. Summary.

An account is given of the topography and major ecological environments of Bardsey, a small island in the north of Cardigan Bay. An outline survey, as a preliminary to a more detailed investigation later, was made. The general faunistic and ecological results of this are discussed.

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STUDIES OF FLUCTUATIONS IN INSECT POPULATIONS

V. THE LEAF-CURLING PEAR MIDGE, *DASYNEURA PYRI* (CECIDOMYIDAE)

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(*With* 1 *Figure in the Text.*)

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1. Introduction.

This is the fifth of a series of papers giving the results of an attempt to study fluctuations in insect populations under natural conditions. References to the earlier papers are given in the third and fourth studies (**2**, **3**).

In the present contribution an account will be given of the leaf-curling pear midge (*Dasyneura pyri* Bouché). This is a multibrooded species and fresh material of full-grown or nearly full-grown larvae has been obtained periodically from Devon. Thus this study is similar to that of the previous one dealing with *D. arabis* in so far as the midge concerned has several broods a year. But it differs because fresh material from the field has been collected for each brood, and so data have been obtained concerning the extent of relative parasitism, in addition to information concerning other inquiline midges. In the *D. arabis* study the midge was bred continuously for 18 generations in an outdoor insectary after the first sample of wild material had been received. In both cases the dates of emergence and number of broods have been recorded for approximately the same period of years.

2. Methods.

Samples of galled leaves were sent to the writer by Mr E. G. Hunt, of Muddlebridge House, Fremington, Barnstaple, whenever requested. Efforts were made to ask for the samples at intervals throughout the year whenever full-grown larvae should have been present in the curled leaves. In this way

samples of the main broods were obtained. The writer is greatly indebted to Mr Hunt for the trouble he has taken to send, or have sent when he has been away, all the material. In addition to collecting the galls, Mr Hunt has from time to time sent information as to the state of new growth of the pear trees, dates of summer pruning and relative prevalence of the midge judging by the presence or absence of galled terminal leaves. All the material has been gathered from his own garden, generally from "William Bon Chrétien", but in times of scarcity from nine other varieties and suckers from a pear stock. Some idea of the actual numbers of midges present can be obtained from Table 5, which shows the numbers reared from the samples.

As soon as the samples were received they were put into lamp-glass cages containing fibre and placed in the outdoor insectary. The emergence of the midges was subsequently recorded, and so the date for sending for the next sample was obtained approximately.

3. Bionomics.

Distribution. The leaf-curling pear midge is widely spread in this country, being recorded from Jersey, Devon, Kent, Surrey, Essex, Hertfordshire, Bedfordshire, Nottinghamshire and Caernarvonshire. Abroad it has been recorded from France, Germany, Holland, Norway, Sweden, Denmark, Switzerland and Italy. It has also been accidentally introduced into New Zealand, where it has become a serious pest. It has occurred recently in New York State, U.S.A. (**4**).

Life history. The eggs, which are red, are laid between the folds of the young leaves as soon as they burst from the bud, up to about 35 eggs being laid on one leaf. The larvae hatch in a few days and, by their action together with the lateral growth of the leaf, the leaves remain curled. A double tube along the mid-vein is thus formed. This gall, at first bright red, gradually blackens and becomes brittle by the time the larvae are full grown. The length of the larval period, 2–5 weeks in the summer broods, varies considerably according to the weather. The mature larvae drop to the ground where pupation in small cocoons takes place in the top few inches of the soil. Occasionally pupation occurs in the galls. The adults emerge after a lapse of about 10–14 days. The last brood of the year, as well as part of the penultimate and sometimes the antipenultimate ones, remain as larvae in the soil throughout the winter, changing to pupae shortly before the emergence of the adults in the following spring. In this country there appear to be from 3 to 4 flights a year with an occasional very small fifth one. In New Zealand 6 generations have been reported.

Host plant. This species is only known to occur on pear trees. It sometimes causes material damage by stunting the growth of maiden trees.

Enemies and parasites. Several Hymenopterous parasites of this midge, including *Inostemma boscii* Jur., *Misocyclops marchali* Kieff. and *Torymus*

abbreviatus Boh., have been found in France. Additional enemies in France are the predaceous Capsid *Pilophorus perplexus* D. and S. and the Anthocorid *Triphleps minuta* L. In England the Anthocorid *Anthocoris nemorum* L. is known to suck the larvae, pupae and adults, while the larvae of a midge, *Lestodiplosis pyri* Barnes, also attack the larvae. In this country the writer has recorded (**1**) *Misocyclops marchali* Kieff. from Kent, Essex, Bedfordshire, Nottinghamshire and Devon. Dr Ferrière has kindly confirmed this identification for me. It is interesting to note that this parasite has also been reared from *Dasyneura arabis* Barnes (**3**) and *D. ulmariae* Bremi. In America a *Polygnotus* sp. (Platygasterinae) and *Zatropis catalpae* Crawf. (Pteromalidae), also identified by Dr Ferrière, have been found in association with *Dasyneura pyri*. An undetermined bug has been recorded (**4**) from this same locality as attacking all stages of the midge.

Inquilines. In the course of this study several inquiline midges have been reared from *D. pyri* galls. They include *Clinodiplosis* sp., *Contarinia* sp. and *Macrolabis* sp. A *Clinodiplosis* species has also been sent me from New York State.

4. Relative parasitism of the midge.

The relative parasitism[1] of this midge (shown in Tables 1 and 2) has been remarkable. Although the midge from this particular locality has been studied since 1927, no parasites were reared until the second brood of the midge in 1930, when 8 individuals of *Misocyclops marchali* Kieff. appeared. Since that date the second broods of the midge in 1931 and 1933 have been parasitised by this species. In addition most of the broods of the midge which over-wintered as larvae in 1930–1, 1931–2, 1932–3 and 1933–4 have also been parasitised by this species. The over-wintering larvae consist of the latter parts of the second brood, the third brood and the fourth brood of the previous year. In 1933 when the emergence of the third brood was decidedly early that part of it which did not over-winter was also slightly (0·9 per cent.) parasitised. It will be seen therefore that in the four years since the parasite, *Misocyclops marchali* Kieff. appeared in 1930, the second brood has been parasitised 3 times, the third brood 4 times and the fourth brood twice. *But in no case has the first brood of any year yet suffered attack by parasites.* The exceptional second brood of 1932 which was not parasitised only partially emerged in 1932, this in itself an unusual feature for this brood. The second brood of 1933 also only partially emerged in 1933.

This freedom of the first brood of the year from parasites suggests strongly that this species of parasite is not yet adjusted to the midge life cycle and develops more slowly. This is supported by the fact that the percentage

[1] Relative or effective parasitism is an expression used to denote the number of parasites that emerge in any brood compared with the number of midges emerging in that brood. This is usually given as a percentage. Thus if 400 midges and 100 parasites emerge, the relative parasitism is 20 per cent.

parasitism (Table 2) has usually been low and has varied so considerably. It would also appear that the parasites have only recently (1930) arrived in this particular garden and consequently have not yet got a proper hold over the midge.

Table 1. *Numbers of* Misocyclops marchali *Kieff. emerging in the different broods of* Dasyneura pyri, 1927–33.

Year	In first brood of *D. pyri*. Emergence always in current year	In second brood of *D. pyri*		In third brood of *D. pyri*		In fourth brood of *D. pyri*	
		A	B	A	B	A	B
1927	0	—	—	—	—	—	—
1928	0	0	—	0	0	—	—
1929	0	0	—	0	0	—	—
1930	0	8	—	0	1	—	50
1931	0	103	—	0	28	0	219
1932	0	0	0	0	10	—	0
1933	0	41	80	3	5	0	0

A = portion of brood emerging the same year as eggs were laid.
B = portion of brood emerging the subsequent year.
(The number of *D. pyri* in each sample will be found in Table 6.)

Table 2. *Percentage relative parasitism by* Misocyclops marchali *Kieff. in the different broods of* Dasyneura pyri, 1927–33.

Year	In first brood of *D. pyri*. Emergence always in current year	In second brood of *D. pyri*		In third brood of *D. pyri*		In fourth brood of *D. pyri*	
		A	B	A	B	A	B
1927	0	—	—	—	—	—	—
1928	0	0	—	0	0	—	—
1929	0	0	—	0	0	—	—
1930	0	1·7	—	0	1·3	—	13·8
1931	0	3·4	—	0	21·7	0	26·5
1932	0	0	0	0	3·0	—	0
1933	0	2·2	78·9	0·9	3·8	0	0

A = portion of brood emerging the same year as eggs were laid.
B = portion of brood emerging the subsequent year.

A further most interesting fact, shown in Tables 1 and 2, is the delayed emergence of the parasites compared with that of the host midge. Frequently that part of a brood of midges which emerges the same year as the eggs are laid is free from parasites, whereas that portion of the brood which emerges the following year is accompanied by parasites (e.g. the third broods of 1930, 1931 and 1932 and the fourth brood of 1931).

5. Number of broods and emergence dates.

This species has several broods a year and the number that occurred in the years 1928–33 can be easily read off from Fig. 1. The numbers show the dates when the different samples of larvae were received, and the solid black lines the dates of emergence of the midges from these samples. Usually the

first flight of the year is in late April and May and is made up from larvae which have over-wintered. Then there is a second flight in June, a third one about August and a fourth flight which usually occurs in late September or early October. In an exceptionally hot year, e.g. 1933, the third flight took place in July and the fourth one was in August. Occasionally also there is a slight fifth flight as in 1931 and 1933.

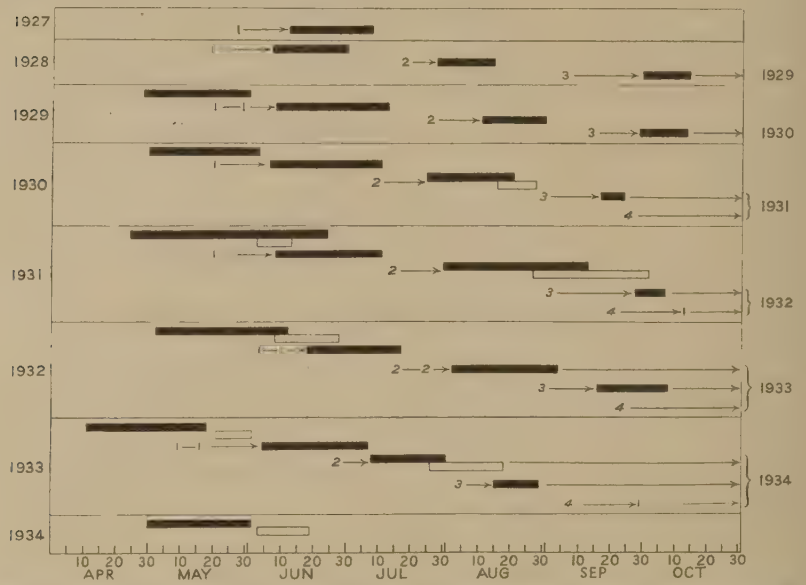

Fig. 1. Number of broods and emergence dates of *Dasyneura pyri* Bouché and its parasite *M. marchali* Kieff. 1927–34. The numerals represent the dates on which the samples of larvae were received, the italicised numerals indicate that parasites will later be shown to be present in the particular samples. The black lines represent the emergence periods of the adults of the various broods, the hollow lines those of the parasites, and the arrows connect the samples with the resulting midges and parasites (see Table 4).

It will be seen from Fig. 1 that the first flight of midges in 1929 and 1930 each consisted of part of the third broods of 1928 and 1929 respectively; that in 1931 contained part of the third brood and in addition the whole fourth brood of the previous year; while in 1932 this flight comprised part of the third brood and only part of the fourth brood of 1931. The first flight of 1933 was made up of parts of the second and third broods of 1932 and the whole of the fourth brood of that year. Finally, the first flight in 1934 consisted of parts of the second, third and fourth broods of 1933.

The proportion of individuals emerging the same year as the eggs were laid and the following year can be seen in Table 3. It is apparent that

under certain conditions aestivation as well as hibernation of fully fed larvae does occur.

The exact dates of receiving the samples from Devon and the dates of the flights can be seen in Fig. 1 and Table 4. The earliest date of emergence recorded is April 11th (1933), while the latest is October 15th (1928).

Table 3. *Percentage of midges in the various broods emerging* (A) *the same year as eggs were laid,* (B) *the subsequent year.*

Year	First brood	Second brood		Third brood		Fourth brood	
	A	A	B	A	B	A	B
1927	100	—	—	—	—	—	—
1928	100	100	0	22	78	—	—
1929	100	100	0	84	16	—	—
1930	100	100	0	?	?	0	100
1931	100	100	0	23	77	0·2	99·8
1932	100	93	7	48	52	0	100
1933	100	98	2	72	28	3	97

Table 4. *Dates of first and last emergence in the broods and flights of* Dasyneura pyri 1927–34, *with the dates* (*in brackets*) *on which the larval samples were received.*

Brood ... Over-wintering*		First	Second	Third	Fourth
Flight ... First		Second	Third	Fourth	Fifth
Year					
1927	—	June 12–July 8 (27. 5. 27)	—	—	—
1928	—	June 5–30 (19. 5. 28)	July 28–Aug. 15 (17. 7. 28)	Sept. 30–Oct. 15 (5. 9. 28)	—
1929	Apr. 28–May 30 (5. 9. 28)	June 8–July 13 (20–29. 5. 29)	Aug. 11–31 (25. 7. 29)	Sept. 29–Oct. 14 (13. 9. 29)	—
1930	Apr. 30–June 3 (13. 9. 29)	June 8–July 11 (20. 5. 30)	July 25–Aug. 21 (8. 7. 30)	Sept. 17–24 (29. 8. 30)	— (24. 9. 30)
1931	Apr. 24–June 24 (29. 8. 30 and 24. 9. 30)	June 17–July 28 (1. 6. 31)	July 30–Sept. 13 (13. 7. 31)	Sept. 28–Oct. 7 (31. 8. 31)	Oct. 13† (16. 9. 31)
1932	May 2–June 12 (31. 8. 31 and 16. 9. 31)	June 18–July 17 (1–10. 6. 32)	July 31–*c.* Sept. 4 (14–26. 7. 32)	Sept. 16–*c.* Oct. 8 (29. 8. 32)	— (22. 9. 32)
1933	Apr. 11–May 18 (26. 7. 32, 29. 8. 32 and 22. 9. 32)	June 4–July 7 (9–16. 5. 33)	July 8–31 (26. 6. 33)	Aug. 15–29 (3. 8. 33)	Sept. 29† (6. 9. 33)
1934	Apr. 30–June 1 (26. 6. 33, 3. 8. 33 and 6. 9. 33)	—	—	—	—

* Consists of adults from the third brood (e.g. in 1929 and 1930), or the third and fourth broods (e.g. in 1931 and 1932) or the second, third and fourth broods of the previous year (e.g. 1933 and 1934).

† One individual only.

It is to be noticed that the number of broods is nearly constant in spite of variations in dates of emergence from year to year. For example, although the emergence dates in 1933 were all early, there were no more generations than in 1931 when all the corresponding dates were considerably later. This

constancy is probably connected with the close association of the midge larvae living on the terminal shoots of pear trees, i.e. on the new growth. In a year like 1933, hot and dry, there was not sufficient new growth to maintain extra broods. In another country, e.g. New Zealand, the climate may be such as to allow growth of the trees to be prolonged and so extra broods of the midge could occur, as they do. In other words there may be a limitation of broods by the length of the period in which new growth can be found on the pear trees. In England late emergences in the summer and autumn would be deleterious to future populations, owing to the fact that probably there would be little or no new growth on the trees on which the succeeding generation might develop. For this reason such late emergences would be biological waste.

Some idea of the fluctuations that have occurred in the various broods and years can be obtained by reference to Tables 5 and 6. For example, the first brood of *Dasyneura pyri* in 1928 was large, so was the second in 1931 and 1933, and the third in 1929; on the other hand the second brood in 1929 and 1932 was small, also the first brood in 1932 was small and comparatively so in 1933. Table 5 indicates (after taking into account the number of samples received and the methods of collecting them) that the midge was most abundant in 1931, less so in 1933 and 1928, and still less so in 1929, 1930 and 1932. However, the present study was not designed primarily to show such reductions or increases in relative abundance.

6. Sex ratio.

In the previous paper (**3**) it was shown that mass breeding of *Dasyneura arabis* would not give a 50 : 50 ratio, but that it was in the neighbourhood of 27 : 73. Table 5 shows conclusively that the sex ratio of *D. pyri* is about 39 : 61. It was further shown (*loc. cit.*) that the first brood of the year in the case of *D. arabis* seemed to have the highest percentage of males, the second brood less and the third and over-wintering the least. In the species at present under consideration, however, the reverse seems to be true (Table 6). Namely, the first brood has the lowest proportion of males, the second higher, while the third and over-wintering broods have the highest proportion. The reason for this is unknown, but the hypothesis put forward when discussing sex ratios in *D. arabis* may explain it. It was, briefly, that temperature may

Table 5. *Sex ratio and numbers of* Dasyneura pyri, 1928–33.

Year	♂♂	♀♀	Total	Sex ratio
1928	702	1306	2008	35 : 65
1929	654	876	1530	43 : 57
1930*	539	906	1445	37 : 63
1931	1722	2573	4295	40 : 60
1932	462	718	1180	39 : 61
1933	1008	1695	2703	37 : 63
1928–33	5087	8074	13161	39 : 61

* That part of the third brood of 1930 which emerged this year was not counted.

Table 6. *Sex ratio of different broods of* Dasyneura pyri.

Brood	Sex ratio	Total emergences ♂♂	Total emergences ♀♀
Over-wintering 1928–9	?[1]	7	18
,, 1929–30	64 : 36[2]	72	41
,, 1930–1	52 : 48[3]	40	27
,, 1930–1	50 : 54[4]	157	155
,, 1931–2	35 : 65[5]	35	66
,, 1931–2	44 : 56[6]	264	341
,, 1932–3	?[7]	5	2
,, 1932–3	47 : 53[8]	150	169
,, 1932–3	?[9]	2	5
,, 1933–4	31 : 69[10]	11	25
,, 1933–4	38 : 62[11]	48	79
,, 1933–4	61 : 39[12]	17	11
First brood (second flight) 1927	28 : 72	66	172
,, 1928	33 : 67	464	955
,, 1929	38 : 62	315	524
,, 1930	37 : 63	323	555
,, 1931	32 : 68	313	673
,, 1932	32 : 68	29	63
,, 1933	21 : 79	53	198
Second brood (third flight) 1928	41 : 59	237	345
,, 1929	38 : 62	21	34
,, 1930	32 : 68	144	310
,, 1931	42 : 59	1202	1687
,, 1932	24 : 76[7]	21	67
,, 1933	38 : 62[10]	687	1111
Third brood (fourth flight) 1928	?[1]	1	6
,, 1929	51 : 49[2]	311	300
,, 1930	?[3]	*x*	*x*
,, 1931	30 : 70[5]	9	21
,, 1932	38 : 62[8]	113	181
,, 1933	34 : 64[11]	110	210
Fourth brood (fifth flight) 1931	?[6]	1	0
,, 1933	?[12]	1	0

Explanation of figuring: [1] partial emergence of third brood, 1928; [2] ditto third brood, 1929; [3] ditto third brood, 1930; [4] whole fourth brood, 1930; [5] partial emergence of third brood, 1931; [6] ditto fourth brood, 1931; [7] ditto second brood, 1932; [8] ditto third brood, 1932; [9] whole fourth brood, 1932; [10] partial emergence of second brood, 1933; [11] ditto third brood, 1933; [12] ditto fourth brood, 1933.

control the rate of segmentation in the unfertilised egg and so determine the extent of development of the egg at the time of entry of the sperm. In addition, that the further developed the eggs are at fertilisation the more males result. If this be so one would expect a higher percentage of males in the warm weather, i.e. later broods.

Nothing is known yet about the sex ratio of families derived from single females in this species.

7. Summary.

1. This is the fifth of a series of papers describing the fluctuations of insect populations. It deals with *Dasyneura pyri* Bouché, the leaf-curling pear midge.

2. A short account of the bionomics of this midge is given.

3. The dates of emergence and number of broods obtained from larvae collected in Devon and reared at Harpenden, Hertfordshire, are shown. The constancy with which minor variations caused by differences in weather conditions become levelled out by the end of the year is notable. A limitation of broods by the length of the season in which new growth can be found on pear trees is suggested.

4. The parasite *Misocyclops marchali* Kieff. is recorded as attacking the second and ensuing broods of the midge but in no case the first brood. This partial adjustment of parasite to midge is interesting. A delayed emergence of the parasites compared with that of the host midge is shown to exist. Both these facts may indicate a recent change of host on the part of the parasite. *M. marchali* Kieff. is known also to parasitise *Dasyneura arabis* Barnes and *D. ulmariae* Bremi.

5. The sex ratio of the various broods is different, as the season advances so the percentage of males increases. This can be explained on the hypothesis that the further developed the eggs are at the time of entry of the sperm the more males result.

ADDENDUM.

Recently, Mr L. J. Dumbleton of the Cawthron Institute, New Zealand, has communicated with the writer and drawn attention to the fact that he too has observed that the first brood of the leaf-curling pear midge is less parasitised by *Misocyclops* than the second in New Zealand. In the 1933–4 season at Nelson the percentage parasitism of the larvae was 7 per cent. for the first brood and 28·7 per cent. for the second (**5**). Mr Dumbleton has also been kind enough to send me the proof of a second paper by him on the parasite, and also given me permission, for which I am grateful, to use any of the information contained therein. In this paper (**6**) it is stated that in Nelson in the 1934–5 season there was a complete absence of parasitism among the larvae of the first brood of the midge, but that in the second there was 32·7 per cent. In Auckland, however, in the same season the first brood was parasitised to the extent of 15–30 per cent. and the second 63–83 per cent. These last-named figures are high compared with the writer's figures of parasitism in England. But it must be remembered that the New Zealand figures are based on larval dissections while the English ones are those of relative parasitism, i.e. the proportion of parasites and midges subsequently emerging. They represent in effect the parasitism after all the factors, lethal or otherwise, during the period of development have had opportunity to take effect. There may well be a differential mortality of host and parasite.

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STUDIES OF FLUCTUATIONS IN INSECT POPULATIONS

VI. DISCUSSION ON RESULTS OF STUDIES I–V

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1. Introduction.

These studies of insect populations were designed primarily to collect information regarding periodic fluctuations as they occur in nature, and secondly, to provide hints of the factors involved (**1**). Thus it was hoped ultimately to amass sufficient knowledge to make possible the prediction of outbreaks of insect pests. The gall midges were chosen as a suitable group of insects to study on a quantitative basis. Five separate yet concurrent studies, involving six species of gall midges and each covering a period of about five years, were undertaken. Each study varied slightly in details. The first (**1**) dealt with two wheat-blossom midges, *Contarinia tritici* Kirby and *Sitodiplosis mosellana* Géhin, as they occurred on the classical field of wheat at the Rothamsted Experimental Station at Harpenden. Normally both these species are single-brooded, yet frequently there is a partial second flight of adults in the case of *Contarinia tritici*. The second study (**2**) was on one of the meadow foxtail grass midges, viz. *Dasyneura alopecuri* Reuter. On rare occasions there is a second flight in this species, but it is really single-brooded and univoltine. In this case the material came from near Aberdeen. The third study (**3**) was on the button-top midge of willows, *Rhabdophaga heterobia* H.Lw., which is multi-brooded. Only the over-wintering brood was studied, and the material was collected on one field of a commercial bed near Leicester. The fourth (**4**) was on the Arabis midge, *Dasyneura arabis* Barnes, which is also multi-brooded. In this case midges were reared in captivity for 18 generations from one

original sample collected in Surrey. The fifth and final study (5) was on the leaf-curling pear midge, *Dasyneura pyri* Bouché, another multi-brooded species. Fresh material for each brood was sent from an extremely localised area in Devon.

Throughout, the insects were collected as full-grown larvae, and the samples reared in an outdoor unheated insectary at the Rothamsted Experimental Station, Harpenden. Each of the studies has now been completed for the initial period of roughly five years, and it is opportune to pause and consider.

It is proposed in this paper to state how far these studies are achieving their object or failing in it, and to discuss the results so far obtained as a whole. It is as well to state at the outset that the studies on the foxtail grass midge, the Arabis midge and the leaf-curling pear midge have been discontinued after the initial period, but that it is proposed to continue the other two studies for an indefinite period.

2. Collection of information about periodic fluctuations of insect populations in the field.

It is perhaps unfortunate that so much of the labour entailed in collecting data is purely routine and consequently unattractive. To ensure real success in a project such as this there should be a team of workers carrying out similar studies on a considerable number of insects, preferably pests, in various districts. Such studies should be continued over a long period. In the present case all the insects, although coming from different districts, were reared in one locality, namely Harpenden.

As a consequence of only one person doing the work it has been necessary to use simple, even crude, methods, and also to limit the number of species as well as samples of insects studied; on the other hand, an element of personal error is eliminated. As a direct result it cannot be claimed that minor fluctuations shown in the data are statistically significant; to ensure this would have entailed far too much work. In other words the methods employed are only sufficiently exact for revealing large increases or decreases in population numbers. In spite of these objections there is no doubt that these studies are proving fairly satisfactory in amassing data concerning periodic fluctuations of insect populations as they occur in the field.

The rapidity with which an insect can assume alarming numbers has been brought out on several occasions. For example, the data concerning *Contarinia tritici* and *Sitodiplosis mosellana* show that there are very considerable rises and falls in numbers from year to year. Additional figures since the publication of the first study are now available for the years 1932–5. Table 1 shows the numbers of larvae of both these species that have been present in the standard sample of 500 ears of wheat during the years 1927–35 inclusive.

Table 1. *Numbers of larvae of* Contarinia tritici (A) *and* Sitodiplosis mosellana, (B) *present in* 500 *ears of wheat on Broadbalk*, 1927–35.

	1927	1928	1929	1930	1931	1932	1933	1934	1935
A	1780	2195	19,265	18,595	19,273	7356	1511	3381	4289
B	715	2043	587	3,746	6,027	3114	319	572	4221

Similarly the population of *Dasyneura alopecuri* reared from 100 heads of meadow foxtail grass rose from 1498 in one year to 4748 in the next (1929) in locality A, and in locality B the number in this latter year was 7565. In no other year of the five during which the study was continued was the average reared population per 100 heads of grass more than slightly over 2000. Thus with the exception of the one year, 1929, when the figures were abnormally high, the average reared population of midges per 100 heads of grass was $1439 \pm 121{\cdot}4$. The figures for the numbers of parasites reared also were shown to vary, giving relative parasitism figures from 38 to 0·7 per cent. In the study of *D. alopecuri* the population numbers were based solely on the numbers of insects reared and not on direct larval counts as in the case of the first study on wheat midges. It was shown that this method of estimating populations, and more particularly damage, by emergence figures was untrustworthy as compared with direct counts. The former method masks whatever mortality occurs during the period intervening between the larval and adult stages of the insect. This possible mortality is the reason why the relative parasitism (i.e. the numbers of parasites, compared with the numbers of host, emerging after the winter) has been studied; under these circumstances there probably is differential mortality also to be considered.

In the third study which dealt with *Rhabdophaga heterobia* a similar procedure of basing population numbers on subsequent emergence figures was adopted. Here again there have been marked changes in the numbers of insects reared. It is hard to believe that such changes can be accounted for solely by mortality between the full-grown larval and adult stages. Additional figures are now available since the publication of the third study, and the figures to date are given in Table 2.

Table 2. *Average population of* 500 *galls of* Rhabdophaga heterobia, 1928–35.

Year	Midges	Parasites	Total insects
1928	1573	1607	3180
1929	1235	2204	3439
1930	341	556	897
1931	840	1323	2163
1932	1480	1662	3142
1933	2810	428	3238
1934	796	633	1429
1935	234	148	382

Both the numbers of midges and parasites have varied quite remarkably. It must be emphasised that only the over-wintering brood has been studied in this instance.

The fourth and fifth studies on the Arabis midge and the leaf-curling pear midge were not designed to show differences in actual numbers, although it is obvious from the data that changes have been taking place from year to year and also within the years, i.e. from brood to brood.

3. Possible factors involved.

Throughout these studies the vast importance of weather appears to predominate over everything else: its component physical factors, such as for example temperature and humidity, seem to underlie all fluctuations. In some cases naturally these factors act directly on the injurious insects themselves, in others they act through the host plants, and in others through their effect on the insects' enemies, e.g. their parasites.

Various hints of the way in which such factors may act have been obtained, and, as was originally intended, subsidiary studies based on these hints have been made. Actually there have been three up to date, namely one on the factors governing emergence (**6**), another on the sex ratio at the time of emergence (**7**), and the other on the segmentation of the antennae (**8**). A thorough understanding of emergence is of the utmost importance in work of this nature, and the segmentation of the antennae has been shown to be closely connected with the food supply of the larvae. Besides these aspects there remain a great many hints which must be further investigated. It is proposed in this section to outline briefly the more striking. In the following paragraphs, various lines of thought suggested by the data already accumulated will be emphasised. While in no way claiming that they are the only solutions to the problems, the view is held that they are logical partial explanations. They are given more with the idea of setting forth probable fruitful lines of research than with any intention of finality.

When the term "weather" is used, one or more of the physical factors comprising this complex is implied.

(*a*) *Effect of weather acting directly on the insect.*

(1) *Sex ratio at the time of emergence.* In the species studied there appear to be definite sex ratios for individual species, e.g. for *Contarinia merceri* Barnes it is *c.* 23 : 77; for *Dasyneura arabis c.* 27 : 73; for *D. pyri c.* 39 : 61; for *D. alopecuri*, *Contarinia tritici* and *Rhabdophaga heterobia c.* 50 : 50. It must be realised, however, that these figures do not necessarily convey the correct meaning, because they are based on large numbers of individuals from different broods and in different seasons. In fact the reverse is more true. *R. heterobia* breeds by means of unisexual families but there is no reason to suppose that *Dasyneura alopecuri* or *Contarinia tritici* does. Again it has been shown that in the case of *Dasyneura pyri* and *D. arabis* the sex ratios of their various broods are quite different. In spite of this, however, it has been possible

on occasion to record sudden departures from the normal sex ratio, e.g. in one instance that of *D. alopecuri* was 25 : 75, in another that of an over-wintering brood of *D. arabis* was 3 : 97.

Again it has been shown that delayed mating in *D. arabis* tends to result in the production of more males than is usually the case. In this connection it is interesting to note that data has been provided indicating that the sex ratios of the various broods of *D. arabis* and *D. pyri* are different. In *D. arabis* as the season advances the percentage of the males decreases; i.e. the first brood of the year has the highest percentage of males, the second brood less, and the third and over-wintering broods the least. In the case of *D. pyri* the reverse holds good: as the season advances so the percentage of males increases.

The day-to-day emergence figures show days on which the expected numbers of one sex have suddenly dropped. For example, from 13 samples of *D. alopecuri* on May 30th, 1928, 259 males and 296 females emerged; on the 31st, 257 males and 25 females emerged; on June 1st, 96 males and 301 females emerged. In this case there was a great decrease in numbers of females on May 31st, but the fall was only temporary, as on the subsequent day more females than were to be normally expected emerged.

Thus it appears probable that on some occasions weather will permanently affect the sex ratio, on others only a temporary setback is incurred. The different responses of the sexes to physical factors should be well worth investigating.

(2) *Dates of emergence and number of broods.* There appears to be little effect of season on the dates between which the majority of the over-wintering broods of a midge species may be expected to emerge. On the other hand, in an early year the insects start to emerge much sooner than in a late one. It is apparently not very wide of the mark to say that the earlier the emergence starts the longer it takes to reach the peak and *vice versa*. Further, such early emergences are not so regular in approaching the peak; there are definite minor crests if the day-to-day figures are examined (**6**).

Such observations have led one to put forward a view that the larvae require a certain more or less fixed amount of temperature to develop from fully fed larvae into adults; when such amount of temperature has been made available, then, under given favourable conditions from day to day, emergences will take place. On the other hand, although favourable day-to-day conditions may occur before such amount of requisite temperature has been received, emergences will not occur. The actual day-to-day emergences seem to depend upon day-to-day conditions to some extent, but finally when the insect is ready the urge is overwhelming, and as a result the crest of emergence is nearly constant. This suggestion of using accumulated temperatures to forecast expected dates of emergence is to receive further attention in the future.

The number of broods in multi-brooded species appears to be remarkably constant. This may be due more to the effect of the weather on the plant and

so indirectly on the insects than on the insects themselves directly. It may be due to the length of the growing season of the plants.

(3) *Activity of adult midges.* Unless the weather is suitable for egg laying when the insects emerge, there is little chance of successful oviposition taking place, because the adult midges are individually so short lived (24–48 hours). Thus although large numbers of imagines may be present, unfavourable weather, such as windy days, may prevent a serious attack from developing. Data concerning day-to-day oviposition numbers over a period of four weeks are given in the study on the wheat-blossom midges. Actually virgin females have been found to live longer than impregnated ones, but it may be presumed that in a natural state there are very few virgins for any length of time. In the majority of cases oviposition starts almost directly after mating, which itself follows closely upon emergence. As there are definite times during the day for emergence in the different species, so there are definite periods during the day when oviposition normally occurs. Some details of the emergence times for several species can be found in the subsidiary study on emergence factors (**6**). Thus it will be realised that unfavourable weather conditions from hour to hour may upset a potential severe outbreak.

(*b*) *Effect of weather acting through the host plant.*

(1) *Adjustment between plant condition and insect development.* The success of midge attacks depends largely on whether the plant is in the right stage of growth when the adult midges are ready to oviposit. For example, *Contarinia tritici* and *Sitodiplosis mosellana* normally emerge, oviposit and die within about 48 hours. They only lay on the wheat ears at the time when the ears are bursting from the sheaths. Normally the emergence of the wheat midges and ears coincide, but in 1933 the wheat ears burst their sheaths about a fortnight earlier than usual, and the midges emerged about three weeks before their normal date. The season had had a different effect on the wheat and the midges. The data show that in 1932 there were 7356 larvae of *Contarinia tritici* present in the sample, in 1933 only 1511; similarly in 1932 there were 3114 *Sitodiplosis mosellana* present, in 1933 only 319. Thus there was a large reduction in numbers, probably due to this lack of adjustment between plant and insect.

The state of the host plant at oviposition time also determines in some cases the form of the gall which results, and even whether the larvae succeed in establishing themselves or not. As has been shown the wheat-blossom midges oviposit successfully only at a definite period of plant growth; *Rhabdophaga heterobia*, on the other hand, makes several types of galls, e.g. lateral bud, button and catkin, depending on the stage of plant growth available (**9**). In the same way *R. terminalis* H.Lw. has been shown to cause two types of gall dependent on the state of the willow growth (**10**). Lately (**11**) it has been proved that *Macrolabis corrugans* F.Lw. seldom manages to establish itself

on cultivated parsnip because of the rapidity with which the leaf buds normally uncurl; yet it scarcely ever fails to attack successfully cow parsnip whose buds uncurl slowly.

(2) *Drought.* The data given concerning *Rhabdophaga heterobia* show a remarkable fall in numbers of both midges and parasites in the year 1930. Instead of the normal 3000 insects from the sample, only about 1000 appeared. The next year there were about 2000, and not till 1932 did the insect population return to the normal 3000. The ratio between the midges and parasites remained nearly constant during this period. It is reasonable to suggest that the drought of 1929 was responsible for this diminution. The willows assumed their winter buds earlier than normal owing to the lack of sap rising sufficiently well to continue the normal autumnal growth. A natural consequence of this would be a severe shortage of food to the inhabitants, i.e. midges and parasites, in the terminal button galls. Actually the willows did not recover their normal height of year's growth until the third year (1932) after the drought.

(3) *Length of life cycle of insects.* From these fluctuation studies the view has been obtained that the first brood of the year completes its life cycle quicker than the second, the second quicker than the third, and so on. Yet this does not hold good always; for example, it was shown that the first brood of *Rhabdophaga heterobia* in 1929 reached maturity in the same time as that in 1930, but was significantly slower than the second brood in 1929 and significantly quicker than the second brood in 1930. The weather acting on the availability of food supply probably is just as much responsible for these changes as it is through its action on the insects themselves.

Further, in the Arabis midge study the methods used have revealed the unexpected fact that relatively more males pupated in the soil than in the galls. Under the circumstances of the experiment this indicated a shorter life cycle in the case of the males. Finally the different proportion from season to season of the last brood of the year emerging the same year is interesting. This occurs in both *Dasyneura arabis* and *D. pyri.*

(c) *Effect of weather acting through its effect on the insects' enemies, e.g. their parasites.*

(1) *Differential effect on host and parasite.* On two occasions there has been a sudden rise in numbers of midges and a corresponding fall in numbers of parasites. In 1929 the number of *Dasyneura alopecuri* was much higher than normal and there were far fewer parasites than usual. In the previous brood, i.e. in 1928, the peak emergence of the parasites was earlier than that of the midges instead of about three weeks later. There had been a different effect on the midges and their parasites. It is considered probable that this alteration from normal relative emergence times of host and parasites was directly responsible for the outbreak of midges recorded for 1929. It has also been suggested that some such reason accounts for the outbreak of *Rhabdophaga*

heterobia in 1933, there being almost double the usual number of midges present and the parasitism being about 14 per cent. instead of between 50 and 60 per cent.

It would certainly repay anyone to study under controlled conditions the possible differential effects of physical factors on host and parasite. Lund (**15**) has recently succeeded in demonstrating under laboratory conditions a differential effect of such factors upon host and parasite in some work on *Trichogramma minutum*. He found that the factors producing death of the parasite were not necessarily identical with those killing the host eggs. In the subsidiary study on emergence factors it has been shown that there seems to be a tendency for the parasites of *Rhabdophaga heterobia* to be less affected by cold than the midges themselves.

(2) *Length of life cycle of host compared with that of the parasite.* In the study on *Dasyneura pyri* it has been recorded that *Misocyclops marchali* Kieff., its parasite, occurred three years in the over-wintering generations, three years in the second generation of the particular year, but not once in the first generation. Further, it has been shown that whereas there was frequently a partial emergence of midges in the late summer only once was there a partial emergence of parasites. This delayed emergence of the parasites tends to show that the parasite's life cycle is longer than that of its host and also indicates only an incomplete adjustment of parasite to host. This may mean a recent change of host on the part of the parasite. Dumbleton (**14**) has, in New Zealand, also observed that the parasite emerges too late to parasitise the eggs which give rise to the first brood of the summer.

4. The prediction of outbreaks of insect pests.

It is much too soon to start predicting outbreaks, but in the case of the wheat-blossom midges advantage has been taken of the Ministry of Agriculture's Monthly Reports scheme, whereby its advisory officers send in observational reports on the abundance or scarcity of certain well-known pests. They used to record *Contarinia tritici* and *Sitodiplosis mosellana* as the wheat midges, and it has been possible to suggest a rhythmic periodic fluctuation (**13**). This gave a peak of abundance occurring about every fourth to sixth year. More recently (**12**), using in addition seven years' data from these studies, a prediction was made that the next peak would be about the year 1937. It remains to be seen whether this is correct or not. The data obtained in 1934 and 1935 have supported it.

5. Summary and conclusions.

It must be apparent that the only basis for such studies as these is a sound knowledge of the bionomics of the species under investigation. Time after time some detail of life history has assumed a greater importance than would have been expected. The methods used reveal the larger fluctuations in

numbers and also have provided a galaxy of hints as to the factors involved. As an indicator of points needing further investigation they are ideal. As a means of collecting data for the forecasting of outbreaks of insects it is felt that these studies will, if continued over a long period, prove satisfactory. They should reveal rhythmic fluctuations, if there are any, as well as irregular ones.

It is claimed that such studies should prove more satisfactory than purely phenological observations, because, although it is possible for one person to deal with only a few species of insects, the information obtained is quantitative and throws out definite hints of the causes of fluctuations in the field instead of merely indicating rises and falls in abundance. This is also true when these studies are compared with experiments carried out under rather arbitrarily controlled conditions. The latter should follow rather than precede such studies.

One aim of the work has been to indicate that, if several workers undertook similar studies, much better and far-reaching results would be obtained. These studies need not be full-time occupations when once the details have been arranged and tried out. There could be a central research station where such studies could be planned in the first instance, as there is a large amount of research work entailed.

It is essential that the subject be chosen carefully. From an economic point of view the insect ought to be a pest, and this should not greatly detract from the ultimate value or interest of the work from wider aspects of biology. Having decided on the insect, methods should be standardised, and while not expecting them to be perfect they might well be allowed to remain constant throughout an initial period of five years or so. By this time the weaknesses in the methods would be apparent, and yet valuable data would have been collected. Then either the study could be stopped, or continued on the same basis or an improved one. This is the point at which the study could be initiated in several localities by several persons.

These studies on gall midges have now reached this stage. Only two of them are to be continued, that on the wheat-blossom midges and that on the button-top midge of willows. Several subsidiary studies suggested by this work are being taken in hand. Preparations are also being made to begin similar studies on other insects, such as the cabbage white fly and some cutworms or surface caterpillars. But before such work can be started the old point of a knowledge of the biology of the insects in question reappears. The methods to be adopted must have their foundation on this.

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THE FOOD AND MIGRATION OF THE PERCH (*PERCA FLUVIATILIS*) IN WINDERMERE

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(*With* 1 *Figure in the Text.*)

1. Introduction.

The results recorded in this paper were obtained while working at the Laboratory of the Freshwater Biological Association between July 1933 and February 1935. The perch (*Perca fluviatilis* Linn.) is very abundant in Windermere and was suitable for an investigation, since it could easily be obtained in sufficient numbers to make observations on its food and migrations possible.

Windermere is the largest of the English lakes, having a length of 10·5 miles (16·8 km.), and a mean breadth of about 950 yards (874 m.). It is a deep lake, the mean depth being about 78 ft. (*c.* 24 m.), and the littoral zone is usually narrow. In addition to the perch the following species of fish are also found in the lake: salmon (*Salmo salar*), brown trout (*Salmo fario*), char (*Salvelinus willughbii*), pike (*Esox lucius*), eel (*Anguilla vulgaris*), minnow (*Phoxinus phoxinus*), stickleback (*Gasterosteus aculeatus*), and bullhead (*Cottus gobio*). Of the larger species, the perch is by far the most common and occurs in the lake in very large numbers. Its average size is small, perch over 8 in. in length being uncommon and those over 12 in. in length very rare. The comparative scarcity of the larger fish is illustrated by Table 1, which shows the size distribution of the perch examined. Various methods were used for the capture of perch, and each of these tended to catch fish of a particular range of sizes. Consequently Table 1 does not represent accurately the actual size distribution of the perch in the lake, but it does illustrate the rapid decrease in numbers of perch more than 5·5 in. (14·0 cm.) long. The comparatively small number of perch less than 4·0 in. (10·2 cm.) in length which was examined is due to the fact that the trap in which most of the fish were caught allowed those less than 4·0 in. in length to escape.

Table 1. *The size distribution of the perch examined, showing both the actual numbers in each size group and their percentages of the total.*

Size of fish: in. ...	1·5	2·0	2·5	3·0	3·5	4·0	4·5	5·0	5·5	6·0	6·5
cm. ...	3·8	5·0	6·4	7·6	8·9	10·2	11·5	12·7	14·0	15·3	16·5
No. examined	7	26	8	12	45	125	96	99	81	35	28
Percentage	1	4	1	2	7	20	15	15	13	6	4

Size of fish: in. ...	7·0	7·5	8·0	8·5	9·0	9·5	10·0	10·5	11·0	11·5
cm. ...	17·8	19·1	20·3	21·7	22·9	24·2	25·4	26·7	28·1	29·3
No. examined	28	21	11	7	6	4	1	1	1	1
Percentage	4	3	2	1	1	1	0·1	0·1	0·1	0·1

The perch examined were caught in three ways:

(*a*) By a trap. This consisted of a cylinder of wire netting with a funnel-shaped opening leading inwards at each end. It proved extremely successful in obtaining the smaller perch, and could be used at any depth.

(*b*) By a seine net operated from the shore. This could only be used in comparatively shallow water, and it was of such a mesh that fish less than 6·5 in. in length could escape through it.

(*c*) By angling. This also was only satisfactory in shallow water and for the larger perch. Most of the larger fish examined during the summer were caught in this way.

The majority of the perch examined were caught in Windermere, but the results from about fifty perch from other lakes in the district are also included, as they appear to be in agreement with the Windermere results.

2. Migration.

The perch were found to show very well-marked seasonal migrations. During the summer they live chiefly in the littoral and sublittoral regions down to a depth of about 10 m. In winter, on the other hand, they inhabit much deeper water, living principally at depths between 18 and 27 m. The migration into deep water takes place during the early part of the winter. In October the fish are still numerous at a depth of about 7·5 m., although they have disappeared from the shallow water, but after this month they are mostly at depths between 18 and 27 m. Table 2 (*a*) shows the results of setting the trap at various depths during the months November to March. The trap was usually put in for twenty-four hours at a time. It will be seen that far more fish were caught in the 18–24 m. zone than in any other.

Table 2. *The number of perch caught in the trap per hour (a) in winter, (b) in summer.*

	(*a*) November to March			(*b*) April to October		
Depth m.	No. of hours set	Catch	Catch per 100 hours	No. of hours set	Catch	Catch per 100 hours
0– 6	116	0	0	86·5	30	35
6–12	172	2	1	157·5	196	124
12–18	90·5	28	31	—	—	—
18–24	223	262	117	73·0	2	3
24–30	74	3	4	—	—	—
30–36	96	0	0	—	—	

The migration into shallow water takes place towards the end of April, and the first large catch made in this region was one of 147 fish at 8 m. on April 28th. After this the perch rapidly became more numerous in the littoral region. Spawning takes place in May, soon after the shoreward migration. In order to collect the spawn and thus locate the spawning grounds dredging was done at various depths and over various types of substratum. It appeared

that spawning took place among the rooted vegetation, particularly *Elodea*, at a depth of about 3 m.

From May to September the perch are extremely abundant in the littoral and sublittoral regions, and are found at any depth from a few cm. to 10 m. Table 2 (*b*) shows the numbers of perch caught per hour at each depth during the period April to October. The analysis of the results obtained with the seine net provides further evidence of this seasonal migration. This net is 3·5 m. deep in the centre and is suspended from the surface. Consequently it will only catch fish which are in the top 3 m. of the water. During the winter months 60 draws were made with this net and only two perch were caught. During the summer only 19 draws were made and these produced 57 perch. From this it is evident that many more perch are present in the shallow water during the summer than during the winter.

The factors controlling these migrations are not very clear. There is an obvious correspondence between the time of migration and the surface temperature of the lake. April, the month during which the inward migration takes place, is that in which the temperature of the lake normally begins to rise. October and November, the months of the outward migration, are the months during which the temperature of the lake falls to its winter value. It is, however, unlikely that temperature is the controlling factor, particularly with regard to the inward migration. Since the temperature of the water at the depth at which the perch spend the winter, i.e. 18–27 m., is very little higher in summer than in winter, and the rise of temperature of the surface water during April is only 2–3° C., it is very improbable that there is any appreciable temperature change at the depth inhabited by the perch. As spawning takes place almost immediately after the shoreward migration, it is more probable that it is the ripening of the gonads which is in some way responsible for this migration.

3. Food.

The only previous publications in this country dealing with the food of perch are those of Southern and Gardiner (1926), and O'Donoghue and Boyd (1934). Of these, the former was only concerned with the extent to which the plankton Crustacea were used as food by the perch, and the latter only contains the results of the examination of the stomachs of ten fish. More attention has been paid to the food of this species in Scandinavia, and most of this work has been summarised by Alm (1922), who concludes that in general the smallest perch feed upon plankton Crustacea, the middle-sized ones upon insect larvae and other bottom-living forms, while the largest perch feed chiefly on small fish. There appear to be considerable local variations in the size at which these changes take place. On the other hand, Nilsson (1921), who examined 81 perch from the Gulf of Bothnia and Lake Mälar, was unable to find any evidence of variation in food with the size of the fish.

Some investigations have also been carried out on the closely related North American species, *Perca flavescens*. Sibley and Rimsky-Korsakoff (1930) found that up to 3·5 cm. this fish feeds upon plankton; while from 5 to 7 cm. it feeds upon small aquatic insects. Relatively few of the perch examined by these investigators had been feeding upon fish. The observations made by Clemens, Dymond and Bigelow (1924) and Sibley (1931) are in general agreement with these results. Rawson (1930), who was able to examine some specimens considerably larger than those obtained by any of the previous investigators, found that they had been feeding upon minnows and crayfish. It thus seems probable that the food of perch varies with the size of the fish. That this may also be the case with other species of fish is suggested by the observations of Sibley and Rimsky-Korsakoff (1930) on *Catostomus commersonnii*, *Eupomotis gibbosus*, and *Ameiurus nebulosus*; and of Clemens and others (1924) on *Catostomus commersonnii*, *C. catostomus*, and *Stizostedion vitreum*. Parrott (1929) considers that the diet of the brown trout (*Salmo fario*) is largely determined by its size, and it is well known that the larger individuals of this species frequently become fish-eaters.

Table 3. *The percentage of perch in each size group which contained each of the important food animals, for the period April to October.*

Size of perch: in. ...		Under 3·5	3·5– 4·25	4·5– 5·25	5·5– 6·25	6·5– 7·25	Over 7·25
cm. ...		Under 8·9	8·9–10·8	11·5–13·4	14·0–15·9	16·5–18·5	Over 18·5
Food animals							
Plankton	*Bosmina*	52	9	5	—	—	—
	Cyclops	54	57	38	10	—	—
	Diaptomus	27	57	17	5	—	—
	Daphnia	10	35	31	22	—	2
	Bythotrephes	2	9	10	10	—	—
	Leptodora	—	4	9	13	—	—
Bottom-fauna	Chironomid larvae	8	10	16	16	13	2
	Chironomid pupae	13	10	13	13	15	14
	Gammarus	4	16	18	20	17	4
	Sialis	—	1	10	13	6	2
	Ephemera	—	—	2	6	10	2
Fish	*Gasterosteus*	—	—	1	2	10	14
	Phoxinus	—	—	—	1	10	26
	Perca	—	—	—	—	2	6
	Unidentified	—	—	1	1	19	24
Number of perch		48	116	127	82	52	51

It was therefore considered desirable to analyse the results obtained from the examination of the stomachs of Windermere perch from this aspect in order to show clearly what changes in food do take place as fish grow. As the perch inhabit entirely different regions in summer and winter the results obtained in these seasons should be analysed separately. Table 3 shows, for the summer period, April to October, the percentage of perch in each size group which contained each of the commonest food animals. A very large number of species have been occasionally found in the stomachs of perch, but the

table includes all those which occurred at all frequently. These have been divided into the three ecological groups which they represent, i.e. the plankton, the bottom-living forms and the fish. This table shows that the animals forming each of these ecological groups are eaten by perch of a distinct size range. Plankton animals are eaten by perch less than 6·5 in. (16·5 cm.) in length, bottom-living forms principally by perch between 4·5 (11·5 cm.) and

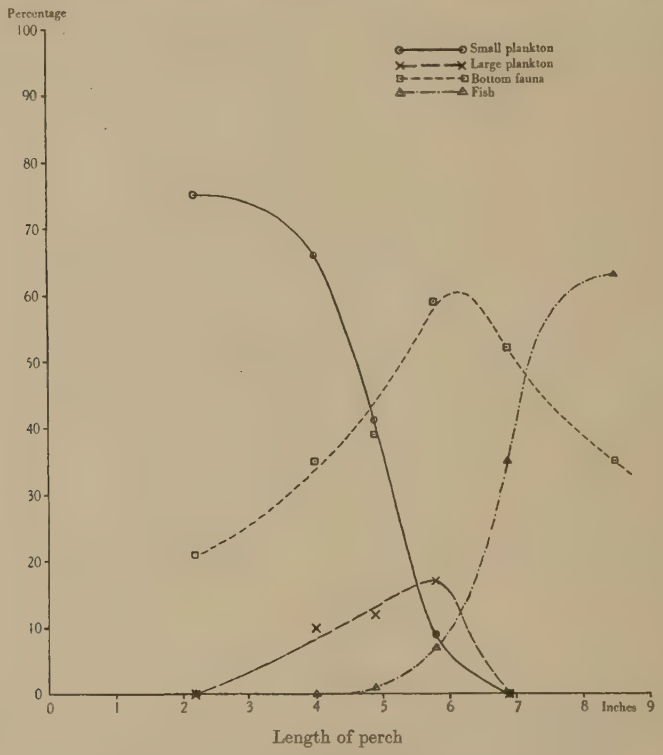

Fig. 1. The percentage of perch containing each type of food plotted against the size of the fish.

7·5 in. (19 cm.) in length, and fish by perch more than 6·5 in. (16·5 cm.) in length. The plankton animals in the table have been arranged in order of size with the smallest at the top, and it is clear that as they increase in size there is a corresponding increase in the size of the perch in which they are most frequently found. Of the various types given in the bottom-fauna section of the table, the Chironomid larvae and pupae are much smaller than the others, and it will be seen that they are eaten freely by perch of all sizes, while the larger forms are eaten chiefly by perch over 4·5 in. (11·5 cm.) in length.

Three species of fish have been found in the stomachs of perch: stickleback, minnow and perch. Of these the stickleback is the least common in the lake and correspondingly is the least frequently eaten by the perch. Although both perch and minnows are very abundant, the former seems to be the more frequently eaten by the larger perch; this is probably because, in general, the perch of all sizes inhabit rather deeper water than the minnows so that the fish-eating perch can obtain perch more easily.

The three feeding stages through which the perch passes are clearly shown in Fig. 1, which represents graphically the occurrence of each of the four main groups of food animals in perch of different sizes. The points upon which these curves are based have been obtained by plotting the mean size of the perch in each of the size groups of Table 3, against the percentage of fish in that size group which contained any animals belonging to the food group concerned. The "small plankton" group consists principally of *Bosmina*, *Cyclops* and *Diaptomus*, and it will be seen that as the perch increase in size these forms become relatively less important than those plankton Crustacea which belong to the "large plankton" group, i.e. *Bythotrephes* and *Leptodora*.

Table 4. *The percentage of perch in each size group, which contained each of the important food animals; for the winter period, November to March.*

	Size of perch: in. ...	Under 4·5	4·5– 5·25	Over 5·25
	cm. ...	Under 11·5	11·5–13·4	Over 13·4
	Food animals			
Plankton	*Cyclops*	75	66	22
	Diaptomus	56	51	10
	Daphnia	25	29	18
Bottom-fauna	Chironomid larvae	3	3	2
	Chironomid pupae	2	—	5
	Chaoborus larvae	2	3	2
	Gammarus	—	2	5
	Asellus	—	—	5
Unidentified fish		—	—	5
	Number of perch	59	68	40

Table 4 shows the results of the examination of perch caught during the winter. Comparison of this table with Table 3 shows that in winter the smaller plankton animals form a more important source of food for the perch over 4·5 in. (11·5 cm.) in length than they do during the summer. The bottom fauna, which in summer forms the chief food of fish between 4·5 and 7·25 in. (18·5 cm.) in length, is in winter hardly represented. It is thus clear that these fish undergo a seasonal change of diet. During the summer they are feeding principally upon the bottom-fauna and upon the larger plankton Crustacea, but during the winter the smaller plankton Crustacea are their chief food. This change can be clearly correlated with the availability of the various food animals. With the exception of *Daphnia*, the larger plankton Crustacea are practically absent from the lake during the winter. The bottom-fauna also is available to the perch during the winter only to a very small extent, since

it is very much less dense at the depth which the perch inhabit at this time than it is in the littoral region. Humphries (*in press*) has found that while the density of the bottom-fauna at a depth of 3 m. is 550 organisms per sq. m., it is only 35 per sq. m. at 12 m. and even less in deeper water. In the absence of these two sources of food the middle-sized perch are thus compelled to eat the small plankton animals to a greater extent than they do in the summer.

Table 5 shows, for the two seasons and two principal size groups, the percentage of perch examined whose stomachs were empty. It shows that perch of all sizes had empty stomachs more frequently in winter than in summer, and that at both seasons the larger perch had empty stomachs more frequently than the smaller ones.

Table 5. *Percentage of fish with empty stomachs in winter and in summer.*

Size of perch: in. ...	Less than 5·5	5·5 and over
cm. ...	Less than 14·0	14·0 and over
Season		
Winter	21	55
Summer	12	23

4. Discussion.

The greater percentage of empty stomachs found in winter might be either because the perch have difficulty in obtaining sufficient food at this season, or because the rate of metabolism and hence the amount of food required falls more rapidly than the rate of digestion as the temperature decreases. Scheuring (1928) has shown that the latter occurs in *Misgurnus fossilis*, and it is therefore possible that this is also the case with perch. There is another reason for believing that this is the cause of the increased percentage of empty stomachs in winter. At this time the majority of the perch are feeding upon the plankton and consequently are eating a very large number of individual animals. If the fish were unable to obtain a sufficient quantity of food they would be looking for it almost continuously, and since the plankton is moderately uniform in its distribution at any one level in the lake they would be feeding almost continually. Consequently the occurrence of empty stomachs would be less frequent, rather than more frequent, than in summer. Thus the increase in the percentage of empty stomachs in the winter is probably due to physiological causes and not to a shortage of food.

The relatively more frequent occurrence of empty stomachs in the larger perch probably depends on the ratio between the size of the fish and the size of the animals upon which it feeds. When a fish is feeding upon very small organisms it will need such a large quantity of them that it will have to feed almost continuously in order to satisfy its needs, and consequently its stomach will be rarely empty. If, however, its food is composed of relatively large organisms it will be able to obtain a large amount of food comparatively

quickly, so that there may be an interval between each feeding period during which its stomach will be empty. It is probable that the impulse to feed upon smaller fish is developed before the fish diet becomes the principal source of food. This is suggested by the fact that out of 52 perch caught on hooks baited with living minnows, 27 were between 4·75 in. (12 cm.) and 5·75 in. (14·5 cm.), and that perch of this size are only rarely found to eat other fish under natural conditions. Since the minnows used as bait were very much easier for the perch to catch than free minnows, it is possible that at this stage the factor which limits the feeding of the perch on other fish is their ability to capture them.

Since the amount of food required by a fish will increase with its size, an increased number of food units will be needed if the food remains the same. As a consequence of this a point will be reached during the growth of the fish at which it will experience difficulty in obtaining a sufficient number of food animals. If this is to be avoided, the fish will need to change its diet so as to take its food in larger units. The two changes in type of food which have been shown to take place in the perch are clearly of this nature. The bottom organisms, which are eaten by middle-sized fish, are much bigger than the plankton Crustacea eaten by the smallest perch, but they are also very much smaller than the fish which compose the diet in the final stage. Actually the sizes of the animals eaten by the perch in the three phases are such that the number of animals eaten per day decreases as the fish grows, although the amount of food required is always increasing with the increasing size of the fish. The saving in time and energy thus obtained is to some extent offset by the greater scarcity and difficulty of capture of the larger food animals.

The benefit to be gained from food changes of this type may be illustrated by a numerical example. The average dry weight of a fish of the size generally eaten by a large perch is about 0·3 gm.; and, since an 8-in. perch will eat about four of these fish a day, its daily food requirements will be about 1·2 gm. dry weight. On the assumption that the amount of food required by a fish is proportional to its weight and so to the cube of its length, a 4-in. perch would need 0·15 gm. of food per day. The dry weight of a *Cyclops* is about 0·000004 gm. (Birge and Juday, 1922), and therefore a 4-in. perch feeding upon these animals will need 37,500 of them per day. This is roughly one every two seconds, and with an animal as common as *Cyclops* it would be possible for the perch to keep up this rate of feeding. An 8-in. perch, however, would need 600,000 *Cyclops* a day, and it is very unlikely that a fish would be able to keep on feeding at the rate this would require, and it is therefore much easier for a large perch to obtain sufficient food if it changes over to some larger food animal.

It thus appears that the perch gains a definite advantage from food changes of the type which have been shown in this paper to take place. Changes of this type, that is, the increase in the size of the food animals with the size of the

perch, seem to take place throughout the life of the perch, so far as it has been investigated. In each of the three principal stages, plankton-feeding, bottom-feeding and fish-feeding, the food animals are distinctly larger than those eaten in the previous stage; and within the first two stages there appears to be a definite tendency for the larger perch to eat the larger species.

5. Acknowledgments.

My thanks are due to Prof. P. A. Buxton, Dr W. H. Pearsall, Mr J. T. Saunders and Mr R. S. A. Beauchamp for their helpful criticisms of the manuscript of this paper.

6. Summary.

1. In Windermere the perch shows a well-marked seasonal migration, living in the top 10 m. of the water in the summer, and at depths between 18 and 27 m. in the winter.

2. In summer the food of the perch changes with the size of the fish: fish less than 5·5 in. (14 cm.) in length feed chiefly on plankton, those between 5·5 and 7·0 in. (18 cm.) in length feed on the bottom-fauna and those over 7·0 in. in length feed on fish.

3. As the perch increases in size, the size of the animals which it eats increases. The animals composing the bottom-fauna are considerably larger than those forming the plankton, but they are also very much smaller than the fish eaten by the largest perch. Within the plankton-feeding and bottom-feeding stages there is a tendency for the larger perch to eat the larger species.

4. In the winter those perch which in summer fed upon the larger plankton species and the bottom-fauna, feed upon the smaller plankton animals. This change occurs because the animals which they eat in summer are not available in the winter.

5. A higher percentage of fish with empty stomachs is found in winter than in summer. Also the stomachs of large fish are more frequently empty than are those of small fish.

6. It is pointed out that food changes of the kind shown are necessary to the fish.

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THE DISTRIBUTION OF THE GREY SQUIRREL (*SCIURUS CAROLINENSIS*) IN GREAT BRITAIN IN 1935

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(*With* 1 *Folding Map.*)

1. Distribution.

After a period of rapid increase and extension of range, the introduced American grey squirrel reached a high density in some areas during 1929 and 1930 (**1**). During the winter of 1930–1 and during 1931 a pronounced reduction occurred in nearly all districts where the squirrels had been numerous (**2**, **3**). Although at this time active measures were adopted by agriculturists, foresters, game preservers and municipal authorities and many squirrels were killed, there was evidence of considerable mortality due to disease which undoubtedly played an important part in bringing the population down to a low level by 1932. Since 1932 there has been no further evidence of disease, and in spite of the fact that a continual war is waged on them, particularly on game preserves, the squirrels appear to have increased in numbers and continued to extend their range during the past three years.

An attempt was made in 1935 to obtain as many records as possible of the occurrence of these squirrels. The map shows every locality from which a report has been received of the presence of grey squirrels during the year ending August 1935. For the purposes of this map records for previous years have not been included but maps based on the earlier data have already been published (**1**, **2**, **3**). The information was obtained in two ways: (1) by correspondence invited through the press, by broadcast enquiries in the course of gardening and farming talks, and through the observers reporting on animal numbers for the Bureau of Animal Population; (2) by a special enquiry carried out by the Automobile Association, whereby all road patrols in Great Britain reported on the presence or absence of grey squirrels in their districts.

Altogether 1385 reports of occurrences in 1934–35 have been mapped, distributed as shown in Table 1. In many cases several reports have been received for the same locality, particularly for public parks and gardens, but only one for each is included for the purposes of this paper. The most noticeable extension of range during the last few years appears to have been a general southward and westward movement from the well-occupied south midland area, several new localities being reported in Hampshire, Wiltshire, West Gloucestershire and Herefordshire. New reports have also been received from Leicestershire, Rutland and Lincolnshire on the north of this area. The few isolated occurrences in Suffolk are interesting and rather puzzling: all

these reports are of single squirrels only, and there is no evidence of many being found in any one locality. I cannot trace any separate introduction in Suffolk, so these squirrels would seem to be wanderers from the main body, probably settling down in Suffolk. The most curious feature of the spread of the grey squirrel is the fact that they have not previously invaded East Anglia, although one of the earliest and most important centres for distribution was at Woburn in Bedfordshire. Essex and Suffolk would seem to have many quite suitable habitats, but even in Epping Forest only an occasional grey squirrel has been seen.

Table 1. *Number of reports of occurrence of grey squirrels in different areas*, 1934–5.

London and Middlesex	59	Gloucestershire ...	58
Surrey	202	Wiltshire	13
Kent	164	Somerset	2
East Sussex	125	[1]Herefordshire ...	7
West Sussex	46	Worcestershire ...	7
Hampshire (North) ...	80	Cambridgeshire ...	4
Berkshire	71	Suffolk	8
Buckinghamshire ...	73	Rutland	3
Hertfordshire ...	46	Lincolnshire ...	2
Essex	3	Bournemouth area	13
Bedfordshire	29	Exeter area ...	12
Huntingdonshire ...	15	Cheshire and N. Wales	42
Northamptonshire ...	47	Yorkshire	110
Leicestershire ...	10	West Scotland ...	16
Oxfordshire	42	East Scotland ...	30
Warwickshire ...	46	Total	1385

Grey squirrels are now reported from localities 10–15 miles around the Exeter centre. Little evidence is available of any great extension from Bournemouth, the squirrels being common in the town and environs, but few are reported in the surrounding country. So far as known the New Forest is still practically free from these squirrels, since the main advance from north Hampshire has not reached it and it has not been invaded from Bournemouth. No further information has been obtained about the grey squirrels kept in a park at Aberdare, Glamorgan: there are no records of them spreading into the surrounding country.

Comparatively few reports are available from the Cheshire-North Wales area, and these seem to be grouped in East Cheshire and the Wrexham-Mold area (around the introduction points in fact), leaving a blank area in central and western Cheshire. This is rather surprising, as these two areas were practically continuous when the distribution was mapped in 1932 (**3**). I have not, however, had time to make detailed local enquiries, so it is possible that this may be due rather to a lack of reports than absence of squirrels. The Yorkshire range is evidently limited by the Pennines on the west, while the Cleveland hills and the wolds do not provide many favourable situations. There is a tendency for a south-westerly movement into the Leeds-Doncaster area. In Scotland many new localities are reported in Fife, arising from the Dun-

[1] A single grey squirrel was reported by Capt. H. A. Gilbert at Garnons Hill, 7 miles west of Hereford, on Oct. 1st, 1935.

fermline centre, but the Dumbartonshire area does not seem to be noticeably larger. Several reports have been received of grey squirrels to the immediate west of Edinburgh, the progeny of escapes from the Zoological Gardens.

The grey squirrels in County Longford, Ireland, have not been included on this map, but they are still present in that area.

2. Numbers.

The points on the map do not, of course, bear any relation to the density of the squirrel population in any given area, since they are merely records of occurrence. Comparable data on the density in different areas is not available, but general correspondence gives the impression that Surrey, Sussex and Kent are the areas most thickly populated by grey squirrels at the present time. Many reports emphasise the observed increase in numbers since the low period of 1931–2. In Table 2 some records are given of the numbers killed on different estates during the past three years: it will be seen that there is a general rise in these figures for 1933 and 1934. Although these areas are very favourable habitats, grey squirrels are trapped and shot continually by the keepers. There seems little doubt that a large proportion of the squirrels killed in Wychwood Forest are not bred in the forest but come in from the surrounding country: the forest is a game preserve and several keepers are continuously trapping and shooting squirrels, while every drey found in the spring is destroyed. There is an interesting field for research in the study of the movements of these animals.

Table 2. *Numbers of grey squirrels killed on four estates during the last three years.* (*The figures are for the year ending April 30th.*)

Year	Burnham, Bucks. (500 acres)	Wychwood, Oxon. (1400 acres)	Alton, Hants.	Garrowby, Yorks.	Total
1932–3	290	450	200	190	1130
1933–4	340	1059	170	301	1870
1934–5	295	1427	225	227	2174

3. Acknowledgments.

My thanks are due to all those who have sent me reports and in particular to the Automobile Association for their extremely efficient co-operation in this survey: and to Mr J. M. Brander, Sir Arthur Hazelrigg, Mr Oliver Watney, Mr George Arnett, Prof. J. A. Scott Watson, Mr C. H. Middleton, The Royal Agricultural Society, and the Forestry Commission for their help in obtaining information.

The data obtained, on which the map is based, are available in the Bureau of Animal Population.

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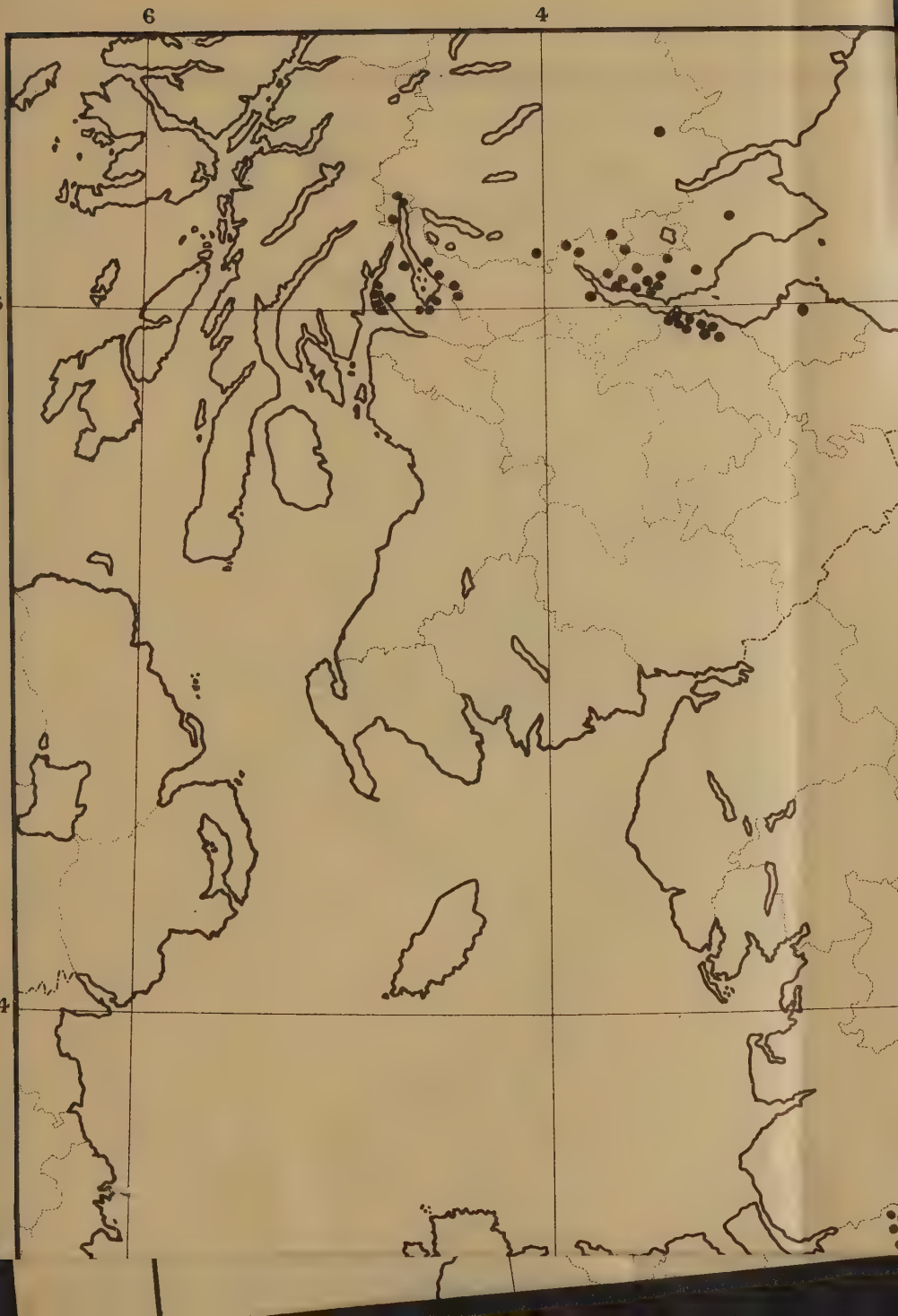
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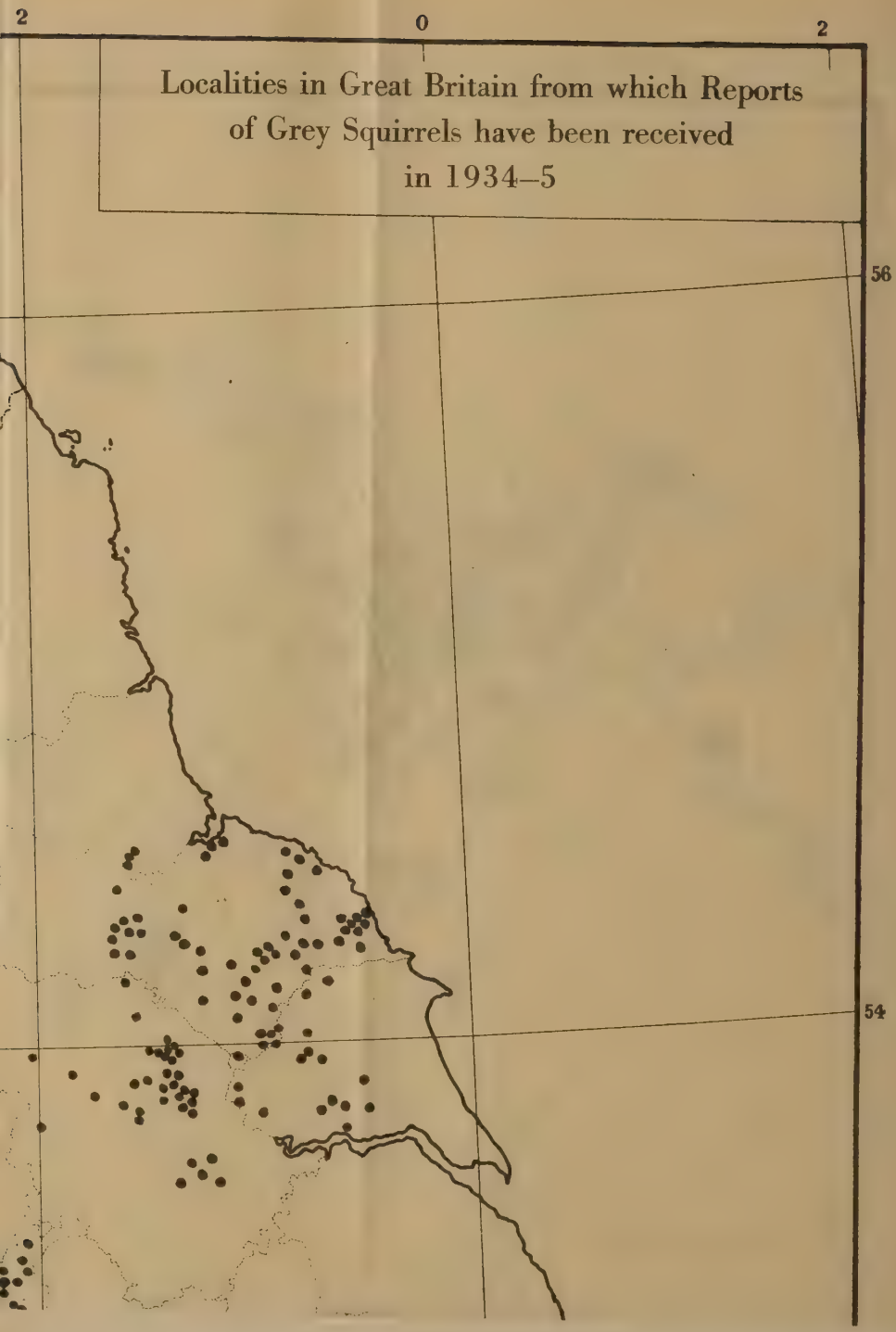
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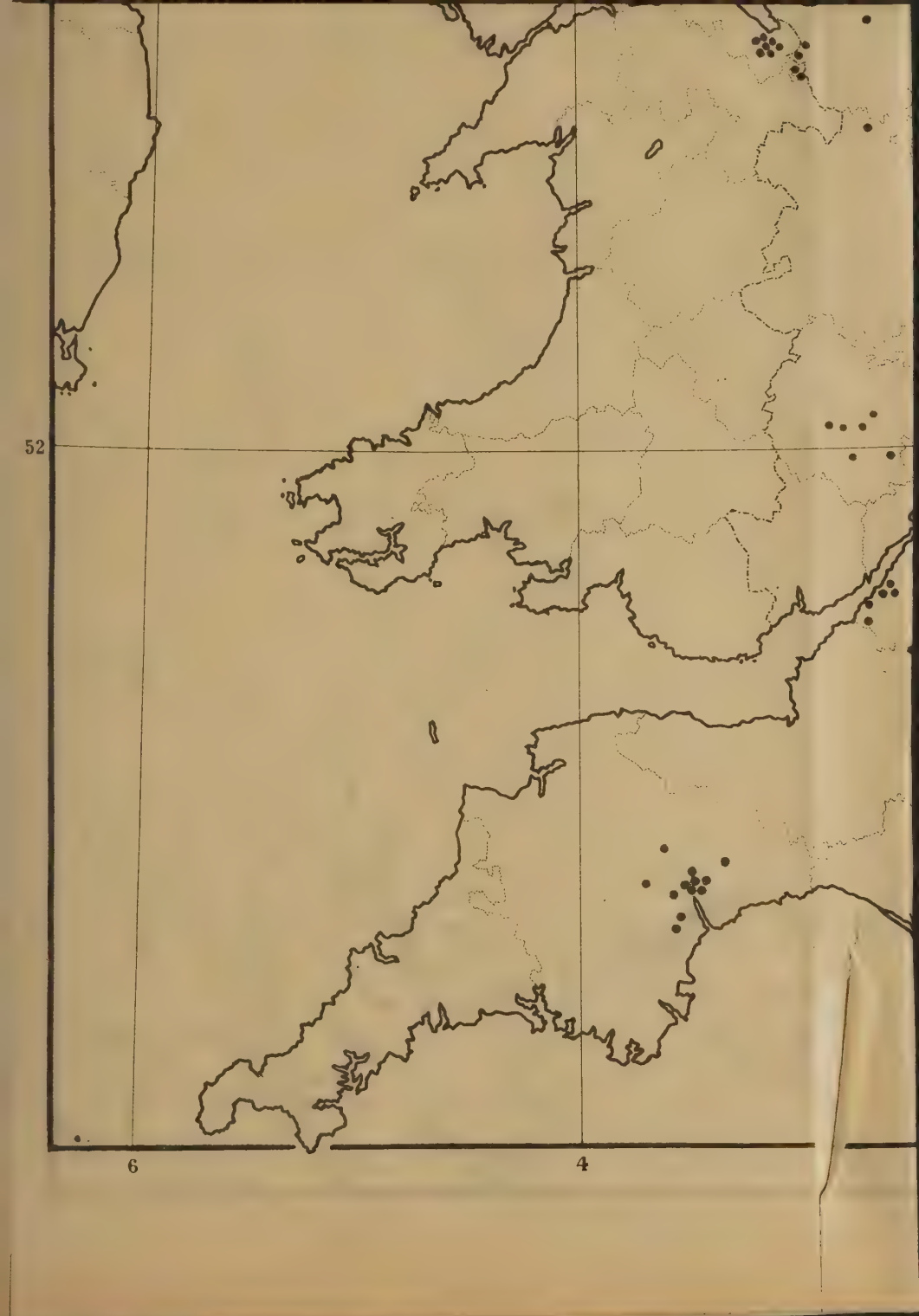
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AN EPIDEMIC AMONG VOLES (*MICROTUS AGRESTIS*) ON THE SCOTTISH BORDER IN THE SPRING OF 1934

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(*With Plate* 9.)

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1. Introduction.

In a previous report by Findlay and Middleton (1934) it was shown that abundance of voles (*Microtus agrestis*) in Argyll (Glenfinart) and North Wales (Lake Vyrnwy) during the winter of 1932–3 was followed by large-scale epidemics in the spring of 1933. The only agent isolated which could in any way be regarded as the cause of this epidemic was a *Toxoplasma* invading the brain. This conclusion was based on the deaths of voles brought into the laboratory at the time of epidemics in the field, the well-marked nervous symptoms before death, the presence of large numbers of *Toxoplasma* cysts in the brains—not found in normal healthy voles—and the production of similar disease by inoculation of unfiltered brain emulsion into healthy control stocks of voles; and, finally, the absence of any evidence that bacteria or filterable viruses were playing any part in the epidemics. The evidence from earlier experiments with wild voles from Oxford (Elton, Ford, Baker and Gardner, 1931) suggests strongly that a similar disease occurs in the south of England in *Microtus agrestis hirtus*. As will be seen, it was *Toxoplasma* that was found to be associated with an epidemic at Newcastleton in 1934. We are justified in concluding that *Microtus agrestis*[1] in the north and probably also *M. a. hirtus*

[1] *Microtus agrestis* is divided into two races. *M. a. neglectus* definitely occurs in Argyll and *M. a. hirtus* at Oxford. The voles on the hills in North Wales and the Scottish Border are most like *M. a. hirtus*, but in some respects intermediate.

in the south are periodically killed off probably by epidemic encephalitis caused by *Toxoplasma*.

Voles have now been proved to fluctuate with a short period of three or four years, in Norway (Collett, 1912; Elton, 1924), Great Britain (Middleton, 1930, 1931 and MS.) and Labrador (Elton, MS.). These fluctuations can now to a large extent be forecast, and therefore offer an important field for experimental epidemiology in the field and laboratory. Considering how little is as yet known of the manner in which epidemics of infectious disease arise either in man or animals, it seems probable that a complete study of natural epidemics such as occur in voles would throw light on the processes involved. Forecasting fluctuations in future should become still more exact, since Goldie (MS.) has discovered a 3–4 year climatic pulsation in Scotland with which the vole cycle is correlated and whose existence had already been deduced from the synchronous periodicity of rodent fluctuations in the North Atlantic area (Elton, 1924, 1929).

In developing this epidemiological study it is necessary to get information about periodicity in numbers, actual densities, breeding potentials, disease organisms and their life history and possible ectoparasite carriers, the general ecology of voles, food factors, immunity, and the manner in which climate affects the voles. The periodicity is usually a 4-year one, with an occasional 3-year period. In the last "cycle" the interval between peaks was 3 years (Argyll, 1929–32; Newcastleton, 1930-3). It will be noticed that some areas lag 1 year behind others. It is very seldom more than this, so that the Argyll epidemic in 1933 made it highly likely that the Newcastleton area (which continued to show vole increase up to high density during 1933) would have epidemics in the spring of 1934. By September it was possible to make a definite forecast of epidemic for the following April.

On the basis of this forecast, work was planned to cover the seven months January to July 1934, in order that conditions could be studied before, during, and after the epidemic. The arrangements included comparative census work monthly, together with trapping each month of live voles to be despatched to London for pathological work. A sample grid census was done just before the epidemic, in order to get some idea of actual density. An ectoparasite survey was done at the same time. The plan worked successfully and gave a clear-cut picture of the sequence of events. Its success depended on four features of organisation without which the study of such wild animal epidemics is inevitably haphazard and usually impracticable: a general intelligence system through field observers combined with accurate sample comparative censuses at chosen stations, facilities for pathological work, and healthy control stocks of laboratory-bred voles.

These vole fluctuations are important in forestry owing to the serious damage caused by voles to young conifers—running in certain years into thousands of pounds. It is also worthy of note that the present epidemic

occurred within the same area as the historic vole plagues of 1875 and 1891–2 which ravaged sheep pastures on the Border. The study of natural control by disease may suggest practical means of artificial control.

2. ACKNOWLEDGMENTS.

The background of this work is a general investigation of vole populations that is being carried out under a grant from the Darwin Fund of the Royal Society to Charles Elton, who has been assisted by D. H. S. Davis. Enquiries carried out by A. D. Middleton under a grant from the Agricultural Research Council have also contributed to the result. The Forestry Commission made a grant for the expenses of the epidemic survey (including special journeys and trapping). We wish to thank Sir John Sutherland and Mr J. M. Murray for the special facilities provided. The care and energy displayed by Mr James Murray, the forestry apprentice in charge of vole trapping, deserve special acknowledgment. The arrangements at Newcastleton were carried on under the skilled supervision of the forester in charge, Mr J. F. MacIntyre, to whom we owe a debt of gratitude for many services. The voles used for experiments were bred by R. M. Ranson at Oxford.

We desire also to thank Prof. E. S. Goodrich, F.R.S., in whose Department the ecological work was centred.

3. CENSUS WORK.

Newcastleton State Forest is an almost isolated area of young conifer plantations set in surroundings of sheep pasture—mainly *Molinia* moor. The planted area in 1933 was about 2020 acres. Owing to the dense cover that grows up in absence of burning and sheep grazing, the forest carries a much higher vole population than the surrounding pastures. Various census observations indicate that during periods of abundance this planted area contains over a hundred thousand but less than half-a-million voles.

The relation of voles to other species of mammals might be of importance in an epidemiological study: we know, for instance, that many ectoparasites and some endoparasites are shared by voles and mice and even by shrews (Elton, Ford, Baker and Gardner, 1931). This has been found to apply also to small mammals in Lapland (Elton MS.). At Newcastleton, however, there is an almost "pure culture" of *Microtus*, and only a very few bank voles or wood mice. There are four sets of facts that prove this:

(1) The 292 small mammals trapped on the epidemic quota areas, January-June 1934, consisted of 270 *Microtus*, one bank vole (*Clethrionomys glareolus*), one wood-mouse (*Apodemus sylvaticus*) and 20 shrews (*Sorex araneus*).

(2) Since the last two species might not normally have entered the live traps in such numbers as the first two, we may add the break-back trap record from J. F. MacIntyre's regular trap-censuses on other parts of the area from

1929 to 1934: *Microtus*, 546; *Clethrionomys*, 32; *Apodemus*, none; *Sorex araneus*, 130. As might be expected more shrews were caught by this method of trapping. All the bank voles, except one taken in 1934, were caught in 1929 and 1930, and their virtual disappearance after the previous vole epidemic in 1931 is of some interest.

(3) Trapping on the older planted area in 1933 gave rather higher proportion of bank voles: *Microtus*, 17; *Clethrionomys*, 2; *Apodemus*, none; *Sorex*, 7.

(4) Further confirmation is given by examination of 23 pellets of short-eared owls (*Asio flammeus*) from the area in 1934. These contained 67 *Microtus* skulls and 9 *Sorex araneus* skulls.

These figures prove that on the younger planted areas (1923 onwards) at any rate bank voles were scarce or absent in 1934, though they may be increasing on some of the older plantations. Wood-mice are practically non-existent. Shrews are quite abundant and use the vole runs. A few moles (*Talpa europaea*) live on the area and surrounding pastures. There are also a few rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*), but these are kept down to very low numbers by trapping. The other mammals found on the area are foxes (*Vulpes crucigera*), stoats (*Mustela erminea*); and occasional weasels (*M. nivalis*)[1], otter (*Lutra lutra*), and badger (*Meles meles*). Rats, hedgehogs and squirrels do not occur. There is a small colony of roe-deer (*Capreolus capreolus*), while sheep occasionally enter the forest, especially on the lower slopes where the epidemic work was done. The occurrence of sheep might have been important, since sheep are subject at Newcastleton to the disease known as louping-ill, and voles have been proved (Findlay and Elton, 1933) to be highly susceptible to the virus.

The most important predatory enemy of voles at Newcastleton is the short-eared owl (*Asio flammeus*). Four pairs were located on the area in the spring of 1934 and studied by Russell Goddard (1934). The relation between the vole cycle and short-eared owl breeding is being watched.[2]

The "trace census" method was used to measure approximate changes in vole density from month to month. This method, of which the technical details will be published elsewhere, gives a measure of the amount of ground occupied by voles, and to that extent some measure of actual density. A wire circle, 2 sq. yd. in area, is placed at a series of points and the presence or absence of fresh vole dung recorded, the final result being expressed as the percentage of points recording fresh dung. Owing to the well-marked run systems and the large amount of dung produced (a laboratory count, for which a 27-gm. female fed on grass was used, gave 1057 pellets per day), and the fact that voles have a regular feeding and resting rhythm throughout the 24-hours (Davis, 1933), the method gives good results. It has been checked in various

[1] One was caught in a vole trap on the epidemic area at the end of June.
[2] See **J. Russell Goddard (1935)**, J. Animal Ecol. 4, 289.

Photo. C. Elton

Phot. 1. Part of the epidemic area on Tweedenhead at Newcastleton, from which May quotas of voles were trapped. Young spruce one to three feet high among dense *Molinia* and other grasses.

ways. A standard interval between census points is used, in order to eliminate unconscious choice of ground. The exact interval does not matter, so long as it is the same for any one census. On the quota trapping areas, a census on about 60 points, 5–15 yd. apart, was done at the beginning of each month, before trapping began. A fresh area was used each month. The site of the work was the lower slopes of Tweedenhead, on a north-east facing slope, whose appearance is shown in the photograph (Pl. 9). The ground is covered with dense grass, mostly tussocks of *Molinia caerulea*, also locally by large patches of *Deschampsia caespitosa*, *Holcus mollis*, and some *Juncus* spp. Growing in this thick grass are young Norway spruce (*Picea excelsa*) and Sitka spruce (*P. sitchensis*) from 2 to 6 ft. high, under whose shelter the voles often nest. The soil is mostly less than 1 ft. or 18 in. deep, mainly peat, and the voles live chiefly in the surface 6 in. and among the grass tussocks.

The trace census results are shown in Table 1.

Table 1.

	Quota areas		Main line		
Date	No. of points	% with fresh dung	No. of points examined	% with fresh dung	Observer
Jan. 8	90	**80**	115	**62**	C.E. + D.D.
Feb. 12	60	**92**	—	—	C.E.
Mar. 8	50	**94**	—	—	D.D.
Apr. 4	50	**70**	175 (Apr. 16)	**38**	C.E.
May 7	60	**65**	—	—	C.E.
June 11	60	**8**	—	—	D.D.
July 18	75	**9**	—	—	D.D.
Sept. 9	—	—	175	**27**	C.E.

The variation in percentages between January and March, in so far as it is not due to errors in the method, is probably due to local differences in density and in the type of ground. The density remained very high until April, when it began to fall. This fall continued until June and July when very low figures were reached, showing that by this time voles had disappeared from something like nine-tenths of the area. The main line includes some unfavourable vole ground and so the figures are lower. The autumn figure indicates that recovery on the lower slopes where the epidemic was studied may have taken place after June. It was not possible to make more frequent trace census observations owing to the fact that each result meant driving 600 miles and using up three days' time for one man.

4. Breeding rates.

The drop in numbers began just when the onset of the breeding season would normally have sent them up. From the investigations of Baker and Ranson (1933) we know that *Microtus* has a well-marked breeding season in Great Britain, the first pregnancies usually appearing in March or April and the last ones in August or September. It varies slightly at each end both

in date and intensity, in different years and places, but the general cessation of breeding in winter is well marked. The only exceptions have occurred in Argyll in 1933–4 and 1934–5. We are here concerned only with Newcastleton voles, for which two sets of figures are available:

(1) Baker and Ranson's investigation, comprising monthly records for the whole of 1930 and 1931, except January 1930 and July 1931. In their paper, separate details are not given for Newcastleton; but their original data are deposited in the Bureau of Animal Population and are re-analysed here. We wish to thank them for the use of these records.

(2) Notes on the voles from trap-censuses carried out in April and September 1932–4 by J. F. MacIntyre, and recorded by Ranson and Davis.

Table 2 shows the monthly litter rates (i.e. average number of embryos per pregnant female).

Table 2. *Average number of embryos per pregnant female. Numbers of pregnant females are given in brackets.*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Baker and Ranson:												
1930	—	0	2·6	3·7	5	4·4	4·3	3·8	2	0	0	0
			(8)	(4)	(6)	(10)	(3)	(5)	(1)			
1931	—	0	0	3·7	5	4·7	?	3·3	3	2	0	0
Trap-census quotas:				(6)	(4)	(12)		(3)	(2)	(1)		
1932	—	—	—	3·8	—	—	—	2·6	—	—	—	—
				(5)				(5)				
1933	—	—	—	4·9	—	—	—	—	—	—	—	—
				(12)				(0)				
1934	—	—	—	3·5	—	—	—	3	—	—	—	—
				(16)				(1)				

The quotas were not spread out evenly through each month, e.g. that for March 1930 was taken in the last days of the month, and gives a slightly misleading impression of the earliness of breeding. The trap-census figures are from the last week of April and of August. The numbers of females examined are small, but the general results seem to be consistent: a very marked seasonal cycle in the number of young per female, which starts about March or April and tails off about September, the maximum being in May. Apart from the suggestive fact that this cycle follows roughly the annual sunshine curves published by Baker and Ranson (1933) and also the seasonal growth of grasses, we do not know how it is controlled. The litter rate is, of course, only one of the components of the potential increase of a *Microtus* population; but it forms a convenient index of seasonal breeding activity for the present purpose, which is to estimate how far breeding had progressed when the 1934 epidemic began.

The data suggest that in April 1934 voles were just starting to breed, and that few or no young would have been born at the time of the April quota census. The trap-census quota taken in the last week of April contained some

voles in a very advanced state of pregnancy, the duration of which is 3 weeks (Ranson, 1934). We may assume, then, that unless breeding began abnormally early in 1934, young voles were numerous in the nests in May. Weaning occurs usually about 2 weeks after birth, so that young voles would normally have been leaving the nest and beginning to enter the traps in the middle or end of May. That this is the normal sequence of events in spring is proved by a study of the weight groups of the 1930 and 1931 vole quotas, which show that the young voles of the year did not begin to be caught in any numbers until June.

The very sharp drop in numbers, however, between May 7th and June 11th shows that there must have been very great mortality among the young voles. This might be due in part to starvation caused by the deaths of the females. The course of events that spring must therefore have been something like this: January and February, females not breeding yet, healthy; March, many females ready to breed (vulva perforate), mostly healthy; April, many females pregnant, epidemic beginning; May, many females with young in nest, epidemic running its course, many young dying of starvation and probably also from the disease; June, most of the old and young gone, epidemic abated; July, August, September, slight recovery, the remnant breeding.

Baker and Ranson have shown that the increase of wild vole stocks during spring and summer is due almost entirely to the breeding of the old voles that have over-wintered. Not many of the young produce litters in the summer they are born, and the litter size is small. This conclusion has been confirmed by a detailed analysis of the weight distribution of Newcastleton voles in 1930 and 1931. A spring epidemic among adults therefore deals a crippling blow to a vole population which already has serious environmental obstacles to overcome.

Although there is only one month's figures for 1934 to show that breeding was not affected by the epidemic, the April figure is fairly significant, as it is based on the last week of the month. It happens also that the previous periodic decline in voles at Newcastleton, which occurred during the late spring and summer of 1931, occurred at the same time as Baker and Ranson's investigations. These show conclusively that litter rates were not widely different from 1930, when voles were on the increase. This point is of importance, since some wild rodent epidemics apparently cause breeding to be greatly lowered. This is recorded by Preble (1908) for the snowshoe rabbit (*Lepus americanus*) in the Athabasca-MacKenzie region in 1905.

Grid census. In order to get some idea of actual vole density just before the epidemic, a sample plot on some ground between the trapping areas and the main census line was trapped out completely in the first 10 days of March. A trace census was first done (March 1st) at 50 points on the area, which covered about 3000 sq. yd. This gave a figure of 72 per cent. for the amount of ground occupied by voles. The corresponding figure on the quota trapping

area on March 8th was 94 per cent. We deliberately chose a place in which voles were not near saturation point, otherwise the correlation with trace census would not have been significant, owing to possible supersaturation, which would still only give 100 per cent. results. A grid of 324 traps was set out, and the area divided into an inner zone (considered to be free from immigration influence) and an outer zone (subject to immigration). After 4 days the inner zone was practically trapped out, very few being caught during the next 4 days. 20 voles caught on the inner area of 1296 sq. yd. gives a density of 76 voles per acre. The outer zone gave 58 voles in 8 days on 1620 sq. yd.—a density of 172 voles per acre; but this higher figure partly results from continued movements in from the edge. If our sample was representative we are justified in assuming that the higher trace censuses of 80–95 per cent. on the trapping areas represent densities over 100 voles per acre, but probably less than 200 per acre. The June and July trace censuses suggest that nine-tenths of the area was denuded of voles—a total mortality running into hundreds of thousands. The astonishing thing is how few voles were observed, or ever have been observed, dying at the surface during the epidemic period. This is in part due to the dense cover, but may also be due to deaths in the nest. Voles have a rhythmic activity of feeding and sleeping, so that only about a third of their time is spent abroad (Davis, 1933). It seems likely that when voles become ill they simply remain in the nests and die there. In future this can be investigated, as it has been found that most voles in the forest nest under the shelter of the young trees, and the nests are easy to find if looked for there.

5. Trapping and transport.

James Murray carried out trapping for 2–3 weeks each month from January to July 1934. A new type of trap was used, the "Dream", a duralumin box trap with wooden floor, which is set in the vole runs. The voles run in and push against a hanging frame which releases the door behind them. A bedroom full of hay is provided for the voles, to minimise deaths from cold, and also some food (carrot). Voles are not attracted much, if at all, by known baits, and their capture apparently depends on entry by chance or curiosity. 168 voles caught were alive when taken away and 102 were dead. This death in the traps has at all times been a practical problem in vole work and must be distinguished from death due to disease. The monthly rates in the traps are included in Table 3. It is assumed that this high death-rate is mainly due to cold, but it may also be partly due to some sort of trap-shock such as has been noticed in the snowshoe rabbit (*Lepus americanus*) our analysis of the daily catches confirms this conclusion. Traps were visited at approximately 8–9 a.m., 12.30–1 p.m., and at 3–3.30 p.m. Thus a large number of voles were liable to remain anything up to 17 hours in the trap. Table 3 shows that practically all trap deaths occurred in this class.

Table 3. *Trap mortality at different periods.*

Time of day	No. alive in traps	No. dead in traps	Mortality %	Approximate possible number of hours in trap
8–9 a.m.	75	99	57	17·0
12.30–1 p.m.	32	1	3	4·5
3–3.30 p.m.	56	0	0	2·5

Certain days when regular visits were not made are omitted. The almost complete absence of deaths in voles not more than $4\frac{1}{2}$ hours in the traps would indicate that dying voles during the epidemic did not go abroad, but remained in the nests. The mortality from this cause was certainly not higher during the epidemic period, in fact it was rather lower (see Table 4). This variation is not explained by the varying proportions caught overnight and by day. Its chief importance lies in the possibility of the resistance of the voles to epidemic disease being lowered by their experience in the traps.

Traps were set at the beginning of each week and visited three times daily for 5 days and then taken up, to be reset in new runways (on the same area) the next week. Each trap was marked with a red-painted stick. Each live vole caught was put into a separate bag and carried back to the storage hut on the area. At the same time the bedroom hay was taken out (both in the case of live and dead voles) and replaced with fresh hay. The old hay was stored in a bag and examined at Oxford for ectoparasites at the end of each month, by means of a Berlese funnel. The object of this operation was to remove and study ectoparasites which might be left in the traps by diseased voles and to reduce chances of infection while in the traps. In actual fact practically no parasites were found at all in the hay.

The number of days that the voles were kept at Newcastleton varied usually from 1 to 4: 90 per cent. were sent after 1, 2 or 3 days. Two voles in May were kept 8 days and another in June for 10 days. The number put into one store box varied from one to nine. 74 per cent. were in batches of six or less.

The live voles were kept in storage boxes, size $2\frac{1}{2} \times 1\frac{1}{2} \times 1$ ft., under cover in a barn or hut. The box was filled with hay or *Molinia*. Food consisted of wheat soaked in water, carrot and hay. At the end of the second day voles were usually transferred to travelling boxes, size $2 \times 1 \times 2$ ft. with perforated-zinc covered air holes (from one to 15 voles per box), and despatched to London. Table 4 gives some of the data about voles during this period, compiled from the schedules kept by Murray. After each lot was sent off the store-box bedding was burned and the box roughly cleaned before being used again. The voles were sent by passenger train to London, a journey of about 7 hours. The history of a vole was therefore something like this: it may have been up to 17 hours, but usually less than about 8 hours in a trap, kept for up to an hour in a bag, placed in a store-box for usually not more than 3 days with usually not more than six other voles, travelled in company with from one to 14 others for up to 15 hours, and then isolated in a separate cage in

the London laboratory. Most of the voles reaching London would therefore have been in captivity for 2–4 days.

Table 4.

	Jan.	Feb.	Mar.	Apr.	May	June
Number alive in traps	30	28	30	36	36	8
Number dead in traps	15	14	20	24	19	10
Trap mortality (%)	50	50	39	40	35	55
Caught overnight (%)	73	62	51	63	71	89
Number dying before despatch	2	0	3	5	9	2
Number dying while travelling	0	2	5	8	6	0
Mortality between leaving traps and reaching London (%)	6	7	26	36	41	25
Number dying after 14 days in laboratory	3	6	12	16	6	1
Mortality during 14 days in laboratory (%)	10	23	54	69	28	16

Even these small figures show that mortality between trapping at Newcastleton and despatch to London rose from March onwards and reached a maximum of 25 per cent. in May. This is not explained by variations either in the length of time they had been kept before despatch, or in the number kept in storage boxes, except that a rather unusual proportion of the May voles were kept 3 days before despatch, whereas the great majority of voles in other months were sent off after 1 or 2 days. In April, however, very few were kept more than 2 days, and the mortality was fairly high in this month. We are probably right, therefore, in concluding that the mortality between the traps and despatch to London mainly reflected the progress of the main epidemic. This is fully confirmed by the results obtained while the voles were kept in the laboratory, considered in the next section.

6. Pathology.

The pathological investigations carried out on the voles arriving in London were similar to those reported in a previous communication (Findlay and Middleton, 1934). Voles which had died were examined as soon as possible after death, while in certain instances animals which were obviously sick were killed and cultures were made of the heart blood, spleen and liver on a number of ordinary laboratory media. In six voles in which aerobic and anaerobic cultures were made of these organs, in only one was a coliform organism isolated from the spleen. No bacteria were found in stained smears from the organs. An examination of Table 4 shows that the mortality dying in transit from Newcastleton to London was low in January and February but was considerably increased during March, April and May, while in June again it fell to zero. In a similar way the mortality during the first 14 days after arrival was low in January and February but rose in March and April. In May the mortality, however, was again low, although the number of deaths before despatch and during transit was the highest recorded. As the method of transport was the same and the conditions in which the voles were placed were identical during the 6 months of the experiment, the figures of mortality

during transit and in the laboratory strongly suggest that during March and April and to a less extent during May, death was due to the conditions under which the voles were living in the wild condition. This is also borne out by the fact that in January and February only one and two voles died during the first 7 days of captivity in the laboratory, while during March, April and June, eight, 15 and four died in the same period of time.

In determining the cause of death the same difficulty was met with as in previous years, namely that voles apparently healthy at night were found dead and very decomposed in the morning. Thus, of the 21 voles which had died in transit, 20 had either been eaten or were too decomposed to allow of any satisfactory examination, while of 44 dying or killed when sick in captivity, 20 were too decomposed to yield evidence of any value. Only 25 voles were thus available on which to establish the cause of the mortality. As previously stated, bacteriological examinations of organs from six voles which exhibited nervous symptoms and paresis similar to those previously described yielded no evidence that bacteria were the cause of the epidemic. Emulsions of these organs filtered through Berkefeld filters and injected into normal voles failed to cause any sickness or mortality, thus failing to provide any evidence of a filterable virus infection.

Apart from one vole which was found to have a liver heavily infected with *Taenia* cysts (also one during April which died 24 hours after arrival and was found to be pregnant), the only parasites capable of bringing about death were, as in previous years, Toxoplasms which were found in 14 out of the 25 voles, in four during March, eight during April, and two during May. As in previous years, the Toxoplasms were found exclusively in the brains. In one instance the Toxoplasms were transferred by intracerebral inoculation through four consecutive passages in voles, after which they were lost. This difficulty in transferring Toxoplasms to normal voles suggests a further possibility as to the cause of the vole deaths, namely, food deficiency. Experiments with Protozoa and helminths of low pathogenicity has shown that liability to infection is increased by dietary deficiencies. It seems, therefore, possible that with increase in numbers the food supply of the voles may become deficient, either quantitatively or in some special factor necessary for pregnancy. A dietary deficiency might thus itself be responsible for a certain number of deaths or might predispose to the spread of a protozoal infection of low pathogenicity. Further work is obviously required in order to investigate this question.

7. Summary.

On the basis of trapping and trace censuses an epidemic among voles (*Microtus*) was forecast in the Newcastleton area of southern Scotland for the spring of 1934. This was expected as the result of a periodic maximum in numbers shown in 1933. Field and laboratory studies were carried out during

the first 6 months of 1934, involving census work, breeding voles, collection of live voles and pathological examinations and experiments. A severe epidemic occurred with a peak mortality in April and May, voles dying in the laboratory with a protozoan infection of the brain due to *Toxoplasma*. This was successfully transmitted to stocks of normal healthy voles and no deaths were found due to causes other than *Toxoplasma*. Since *Toxoplasma* was found to cause similar mortality on two other areas in 1933 it is evidently an important controlling factor in the short-period fluctuation known to occur among vole populations in Britain.

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A CENSUS OF SHORT-EARED OWLS (*ASIO F. FLAMMEUS*) AT NEWCASTLETON, ROXBURGHSHIRE, 1935[1]

By T. RUSSELL GODDARD.

(*Hancock Museum, Newcastle-upon-Tyne.*)

It was shown in a previous paper (*J. Anim. Ecol.* 4, 113, 1935, which contains a map of the area) that at least three but not more than four pairs of short-eared owls nested on this area in the spring of 1935, at a time of vole abundance. I spent the whole of April 15th, 1935, on the forest at Newcastleton and walked over the most likely areas for owls. I had heard from Mr John F. MacIntyre, the forester, that an owl had been seen in the neighbourhood of Kaim Cleuch this year, so I searched both branches of this cleuch thoroughly, beating all patches of dried bracken and other suitable nesting sites, but without result. I also searched Muckle Punder Cleuch thoroughly but saw no traces of owls there. Although I spent the whole of the day on the southern slope of the forest, which was the area favoured by owls last year, I did not see a single owl.

On April 26th I went to Newcastleton again and devoted the whole of the two following days to searching for owls. I spent the whole of April 27th walking over the southern slope, and again I searched thoroughly all the likely nesting sites in Kaim Cleuch, Muckle Punder Cleuch and other smaller cleuchs and bracken patches in that neighbourhood. Throughout the day I did not see a single owl on that part of the forest. On my return through Plantation 26 in the late afternoon, however, I saw a short-eared owl quartering the ground there. I watched it for some time through my binoculars and noticed that it was in moult and was minus one or two secondary feathers in the left wing.

I spent April 28th quartering the south-western area of the forest, paying special attention to that portion lying between the footpath to Kershope and the western boundary fence of the forest. Two pairs of short-eared owls had nested in this area last year. I searched all bracken patches and other likely nesting places on both sides of Muckle Thwarter Gill and also the bracken, rush (*Juncus*) and other coarse vegetation near the boundary fence. I did not find a nest nor did I see any sign of owls until shortly after 1 p.m., when a short-eared owl flew over Muckle Thwarter Gill. This bird, which was quartering the ground, came quite close to me and remained in the vicinity for some time. I observed it closely through my binoculars and found that it was in moult and minus one or two secondary feathers in the left wing, obviously the bird I had observed over Plantation 26 the previous afternoon.

Mr D. H. S. Davis, who was assisting Mr Charles Elton with his vole work,

[1] Publication of the British Trust for Ornithology.

told me that he had seen an owl once or twice in various parts of the forest this year, and the forest workers also reported having seen owls on several occasions either in the neighbourhood of Kaim Cleuch or Plantation 26, but I could obtain no definite evidence of two owls being seen in the air at the same time. Furthermore, no short-eared owl's nest was found this year by the forest workers. The owl I saw and was able to identify was obviously quartering a very considerable area of the forest in search of food, and it was observed hunting during hours of the day when these birds are usually resting when food is plentiful. This bird may have had a mate, which escaped observation, for it is impossible to beat every square yard of the forest in the time available.

Later Mr Carruthers reported that on July 12th he saw two young short-eared owls near to the cattle shed on Plantation 34, that is to say about 150–200 yards west of Muckle Thwarter Gill. He handled the two young birds, which could only just fly. This suggests that they had not come on to the area from outside, but had been hatched not far away from where they were found.

The evidence collected suggests that not more than one pair of short-eared owls bred on the forest this year. A fall in the number of owls frequenting the forest during the spring and summer of 1935 was anticipated in view of the state of the vole population. Mr Charles Elton informs me that there has been a marked decrease in the number of voles (*Microtus agrestis*) since August 1934 and that in May 1935 they were extremely scarce, more so than at any time during the last four years.

Summary.

Whereas in 1934 at least three pairs of short-eared owls nested on the forestry plantations at Newcastleton, it is probable that not more than one pair nested there in 1935. This decrease is correlated with a big decrease in voles during the spring and summer of 1934.

NOTE

THE FOOD OF A BADGER (*MELES MELES*).

In the early morning of July 17th, 1935, a badger was found dead on the road at Boar's Hill, Oxford, apparently killed by a car while crossing the road which runs by the side of Bagley Wood. It was a male weighing 29 lb. The stomach and intestinal contents were examined by Charles Elton and myself and the following were found:

4 hedgehogs (*Erinaceus europoeus*).
4 young rabbits from nest (*Oryctolagus cuniculus*).
4 young mammals unidentified.
Numerous bee cocoons with bees and larvae (*Bombus lucorum*).
1 beetle (*Carabus* sp.).

All the mammals were in the stomach which was very full and had been burst by the impact with the car; some of the bees were in the intestine. The hedgehogs were easily identified by feet, fur and spines, and all appeared to be adults. The badger seemed to have exercised considerable skill in taking only the inside edible portions of the hedgehogs, as only three or four spines were found in the stomach. The young rabbits were all of the same size (3 or 4 days old) and were decapitated. It seems obvious that they had been taken from a nest. The other young mammals were much mangled but may have been water voles or moles: they were very young and must also have been taken from a nest. The cocoons with fully developed bees and larvae identified by Dr B. M. Hobby, indicate that a nest of bees had been attacked by the badger. The intestine was 22 ft. long but contained no worm parasites of any kind.

A. D. MIDDLETON.

REVIEWS

THE AUGUST ISSUE OF THE *JOURNAL OF ECOLOGY* (VOL. 23, NO. 2, AUGUST, 1935)

This issue contains 13 papers of very various nature and length. Mr Ewen Cameron contributes a very careful and thorough study of the ragwort (*Senecio jacobaea*) and its insect parasites, undertaken with the object of finding suitable parasites to export to New Zealand for "control" of the ragwort which has there become a troublesome weed dangerous to stock. Another paper dealing with a single species is Mr Wiehe's experimental study of the influence of the tide on the death-rate of seedlings of *Salicornia europaea*. Dr C. L. Newcombe gives an account of the factors affecting the mixed communities of plants and animals in the intertidal zone on the coast of New Brunswick. Mr Ronald Good describes the complex successions on wet and dry sandy soils at South Haven peninsula in Dorset, a specially interesting area because the history of land accretion is known in some detail from ancient maps.

Two very different regions are described by Mr Eggeling and by Messrs Anderson and Falk, respectively—a papyrus swamp in Uganda and the central desert of Iceland. The Uganda swamp is being drained and afforested with *Eucalyptus*, which is showing very successful growth. Fairly complete lists of the plants and animals of the extremely inhospitable Icelandic region are given. Mr J. G. Myers briefly describes the longitudinal zonation of undisturbed primitive vegetation—i.e. from the mouth towards the source—along the banks of some rivers in Guiana. Prof. McLean contributes an interesting note on an ungrazed maritime grassland in South Wales, dominated by *Festuca rubra*.

Dr G. H. Bates shows that the vegetation of British footpaths traversing the most various types of soil and vegetation is astonishingly uniform (dry sands are an exception), and successfully analyses the constant factors which make it so. Messrs Marsden-Jones and Turrill present the third report on the transplant experiments at Potterne. Dr and Mrs Godwin and Mr Clifford consider the factors at work in the evolution of fens, based mainly on an examination of the peat and its micro-fossils at Wood Fen, near Ely, which is part of an extensive scheme of investigation by the Fenland Research Committee.

Prof. Phillips expounds the organicist view of the "biotic community", which, in agreement with Clements, he calls a "complex organism", and two of his pupils, Messrs Murray and Glover, contribute a description of a conveniently designed frame for listing quadrats in veld grassland.

Reviews include Mr Elton's of the May issue of the *Journal of Animal Ecology*, and notices of *A Botanist in Ireland*, of works on the origin of Mediterranean vegetation, tropical soils and eco-climates, and a Russian outlook on modern phytosociology.

A. G. TANSLEY.

MICRO-CLIMATES.

T. W. Kirkpatrick. *Studies on the ecology of Coffee Plantations in East Africa.* 1. *The climate and eco-climate of Coffee Plantations.* 66 pp., 34 figs., 32 tables. The Crown Agents for the Colonies, London, 1935. Price 5*s.* post free.

Biologists have for some time been aware that "climate" as defined by the meteorologist is a rather abstract concept bearing only a very rough relation to the climate (micro- or eco-climate) of the places where most animals actually live.

It is not, however, mere inertia that has retarded the development of research into the significant climates. There are two very real difficulties in such a study. There is first the difficulty of instruments; those at present available are not suitable for really small habitats, and, in addition, many of them have considerable practical drawbacks in the field. Secondly, there is the difficulty arising from the multiplicity of microhabitats. This means that the worker must either spend his whole time studying the climate (as in the present paper) or make so few eco-climatic measurements that it is very difficult to generalise.

The paper under review includes probably the most elaborate study of eco-climatic conditions ever made in a habitat of any complexity. Even a coffee plantation, however, especially when weeded, is a simple habitat compared with a wood in which there are several strata of vegetation. What must be regarded as the main purpose and achievement of Kirkpatrick's work is to show how far the eco-climate can be correlated with and predicted from the "standard climate". He has been able to show that the correlation is fairly high, and that if sufficiently numerous and varied measurements have been made, considerable accuracy of prediction may thereafter be attained. Various complicating factors, such as local topography, presence of shade trees, etc., can be brought in one by one, and, while the relation between standard and eco-climate cannot yet be reduced to an algebraical formula, the tables (especially Table 21) enable one to fix the eco-climate within quite narrow limits.

The linking up of such research with the actual behaviour of animals (especially insects) would be an absorbing study. Except under the simplest conditions, a wide range of eco-climates must be available within a short distance. It is clear that insects (at any rate in part of their life history) usually find the climate most suitable to them by means of small-scale migrations. In this way, the importance of the eco-climate is, in a sense, minimised; the insect can find a suitable habitat in one place or another, and it is only the persistent effects of the standard climate that cannot be avoided.

Mr Kirkpatrick promises further publications dealing with such questions as these and with the general effects of climate on insect numbers. His next paper will be eagerly awaited by many entomologists.

O. W. RICHARDS.

THE BIRD-LIFE OF AN EASTERN COUNTY.

David Lack. *The birds of Cambridgeshire: with an account of the birds of the undrained fen by H. C. Darby.* 118 pp. and one general vegetation map. The Cambridge Bird Club, 5*a* Market Hill, Cambridge, England, 1934. Price 7*s.* 6*d.*

The second half of this book follows the accepted lines of county bird books, giving notes on the distribution, numbers, migration, etc., of each species. The first part, however, represents a considerable advance on the older methods of presentation, in treating the bird fauna as a shifting one. Readers of Lack's paper upon habitat selection among birds (this *Journal*, 2, 239) will not be surprised to find the environment of birds in the district treated in an interesting manner. The broad habitats are described: chalk uplands, clay lands with their richer woodlands, river valleys, the fenland, the Breckland, open waters, and the sewage farms. There is an historical note on the undrained fenlands and on decoys formerly used in sport.

It seems rather a pity that the opportunity was not taken to include references to the more important vegetation and other ecological surveys carried out in the district, for we have now available a more exact ecological account of at any rate some plant and animal communities than might be supposed from reading the book.

The changes in bird life during the last hundred years or so are sketched: a decrease in some 20 per cent. of the species is noted, in part due to the draining of fens, and in part to changing methods or distribution of agriculture (the stone curlew, corncrake, quail, and

in part the great bustard), also to human persecution. Decrease in certain other species (marsh tit, tree pipit, spotted flycatcher, wood warbler, redstart, and wryneck) remains unexplained. There have been fluctuations in the magpie (in part due to war-time cessation of persecution by keepers), in long-tailed tit and goldcrest (due to the cold winter of 1917) and in the redshank. Two introduced species (red-legged partridge and little owl) have spread over the district, while the goldfinch, jay, green woodpecker, short-eared owl, tawny owl, dabchick, common snipe, garganey, and shoveler have increased, or probably increased.

Certain winter visitors (e.g. hooded crow and dotterel) are now very scarce, while twite and siskin have apparently decreased. The crossbill is increasing. Migration is discussed at some length, the author rejecting the notion that Cambridge lies on any specially narrow migration route. There are now about 96 regular breeding birds of which some 30 are summer visitors. There are 30 winter visitors, and 26 passage migrants. In addition there are some 96 less regularly occurring species.

The authors are to be congratulated on this competent effort to unfreeze the established tradition of producing a handbook over-weighted with unessential details. The book is clearly and competently written, and gives the known ecological data (which are still limited and somewhat vague) in a concise fashion. It may be taken as a good example of the present trend of ornithology.

CHARLES ELTON.

POPULATION THEORIES.

(1) **G. F. Gause.** *The struggle for existence.* 1–163 pp., 9 tables and 41 text-figures. The Williams and Wilkins Co., Baltimore, 1934. Price 13*s.* 6*d.*

(2) **Royal N. Chapman.** *The causes of fluctuations of populations in insects.* Proc. Hawaiian Entomological Society, 8, 279–92, 1933, 5 text-figures.

(1) Charles Darwin laid the foundations of animal ecology, in the third chapter of the *Origin of Species.* He meant to write a book on the struggle for existence, and he undoubtedly foresaw seventy years ahead many of the important branches of ecology: animal interrelations, the influence of animals on plant succession, competition among animals, their immense biotic potential, their occasional escape from checks, and even periodic fluctuations. The last problem he could only see dimly at that time.

Dr Gause has written a book in which he summarises the progress so far made in analysing quantitatively the struggle for existence. He gives an introduction which places the subject in its setting, acknowledges the importance of Darwin's work, and stresses the value of exact experiments on animal populations. Referring to the challenge already thrown out by mathematicians such as Lotka and Volterra, he points out the need for experimental testing of these theories—the most important of which concern the division of available energy resulting from competition between two species with similar food habits, and the oscillations resulting from predator or parasite prey relationships. In both types of reaction we have to study the growth of populations, their limits, and their possible decline either to extinction or to a minimum followed by rise once more. Let us consider some of these phases in the light of Gause's work. First there is often a lag, not only in actual increase but in rates of increase. The lower rates of increase at low densities have been extensively studied and correlated by Allee. Gause pays little attention to this phase, which has also received attention from bacteriologists (although he is clearly aware of its importance), but concentrates on the increase phase. He studied populations of yeasts and Protozoa—these are the testing instruments he uses, and they possess not only technical advantages (and difficulties, which he has brilliantly overcome), but they also approach more nearly than larger animals the actual nature of the differential equations which are used to formularise their behaviour.

The first increase follows geometrical progression, and the logarithms of the population increase give a straight line. This slows down and flattens out, leading to ultimate decrease.

In yeasts the limitation of increase is caused by accumulation of alcohol which kills the new buds; in *Paramecium* the causes are less obvious but assumed to be due to limitation of food supply (bacteria in this case). The absence of precise data on this problem is noted by Gause: he overcomes the difficulty by standardising conditions so far as possible. It seems likely that the techniques developed in the study of water-flea cultures would supply some hints about improving this part of the work.

The curve, up to the point where it has flattened out, is conveniently defined by the logistic curve developed by Pearl and his associates. It does not, of course, represent what takes place in all instances in nature. For one thing, the increase phase in many vertebrates is brought to a close catastrophically by epidemic disease rather than by a gradual slowing due to food shortage. On the other hand, the experiments bring out the important point that many animal populations tend to be self-regulating through various means: another good example is the flour weevil (*Tribolium*) whose numbers are limited by cannibalism among other things. Gause uses figures not only for populations but also for *total biomasses*, an idea already developed by other workers.

A word about mathematics: Lotka and Volterra (and earlier Ronald Ross) have provided us with some very important techniques, through brilliant development of certain differential equations. Gause is able to show that these fit a number of actual phenomena, but are not to be regarded as explanations of all population problems. They are weapons, not explanations. It is clear, for instance, that equations connecting the surface-volume relations with the temperature of a mouse a hundred yards long would be possible. They would not be directly much use. They might, however, throw important light on an imaginary limiting case. They would have to be brought into relations with biological facts. Volterra has already pointed out that mathematical hypotheses have outrun the limits of ecological verification—this gap Gause has done much to fill.

The predator-prey relationship, according to the theories, leads to oscillations in the populations. It depends on the assumption that any population of prey reaches a limit, is caught up by the predator, decreases to scarcity at which the predator starves, and then recovers again. This does happen in nature, but Gause has verified it in the laboratory, in a series of experiments which we cannot treat in detail. He also showed that if a predator is *too efficient* it wipes out the prey and starves, so that periodic oscillations are prevented after one "cycle". This brings out the immense significance of adaptations between predator and prey and points the way to a new synthesis of the older nineteenth-century and the modern outlooks on ecology—a synthesis which would carry Darwin's theories a real step forward.

In other words, for a population to survive, the predator-prey balance of adaptations must be properly adjusted. That catastrophes due to bad balance do occur is shown by the complete extinction of snowshoe rabbits during a periodic epidemic on the Magdalen Islands (Gulf of St Lawrence) in 1906–7, and by the local extinction of a rare vole colony in Manitoba by weasels, noted by Stuart and Criddle. This idea is inherent in my own discussion (1927) of the optimum population, a concept adapted from human economics but not clearly brought into relation with other ideas. We might claim for successful animal populations the same moderation that characterised the monastery of Chengri-la in Hilton's *Lost Horizon*: "We believe in moderation; we are moderately good at escaping from enemies, moderately good at breeding, and moderately good at catching prey."

Here A. J. Nicholson's theories of random searching at different densities could have received greater attention, since they are vital to understanding of the factors preventing a predator from wiping out its prey during periods of scarcity. A practical instance of such a relation in the economic sphere is the present status of muskrats in England, which still require a large body of trappers to catch them although so scarce themselves. Biologically such a system would be uneconomic and the predator would turn to some other prey.

Dr Gause's book should be studied by all ecologists. It is alive and full of fresh viewpoints supported by a rich array of facts.

(2) Prof. Chapman's experiments on the flour weevil are well known to ecologists. He found that a population of *Tribolium* kept under constant conditions with periodically

renewed food supply reaches a constant point through cannibalism and other factors. The present paper surveys the work that has been done in relation to Volterra's theories and gives the results of accidental introduction of a Protozoan parasite into the population of weevils. The parasite set up oscillations—epidemics, really—which are analysed in a very interesting manner. Chapman concludes that he has verified several of Volterra's postulates. There is nothing remarkable in the development of periodic epidemics, however: the value of the work lies in the quantitative analysis of the situation under controlled conditions. One point of great interest is that the maximum points of the oscillations which take place after parasites are introduced are all *lower* than the original constant level of population.

CHARLES ELTON.

THE STUDY OF FRESH WATERS.

Paul S. Welch, *Limnology.* 471 pp., 46 figs. McGraw Hill Publishing Company, Ltd., London, 1935. Price 30*s.* net.

The author of this admirable addition to the McGraw Hill Publications in the Zoological Sciences is the Professor of Zoology in the University of Michigan, and is one of that band of American limnologists which during the present century has found such a fruitful field of study in the lakes of the northern States. As is at present inevitable, the greater part of the book is devoted to the discussion of lakes, though ponds and rivers are briefly described.

A brief introductory section gives a general account of the history of limnology, the extent and nature of the problem, and the geographical data which are a necessary preliminary. The second part deals with the physical and chemical nature of fresh-water environments, including not only the water itself but the lake basin as well. Upon a well-presented basis of the density, viscosity and thermal properties of water is developed the story of the thermal stratification which is so important a feature of many lakes of the temperate zone, and the energy relations of this phenomenon are very clearly described. The importance of the study of the penetration of light is well shown both in the text and by diagrams. There is in this section (p. 76) a curious statement that in some highly coloured waters the amount of red radiation may equal *or even exceed* the total radiation. This is repeated on p. 352 where bog lakes are under discussion, so one cannot regard it as a slip. It cannot be taken literally, but the true meaning is hard to discover. The discussion of chemical conditions ranges over a wider field than what are sometimes called "substances of biological importance", though these naturally receive most attention. The variations in the amounts of dissolved oxygen and carbon dioxide at different depths throughout the year are described, and the account of the carbon dioxide-bicarbonate-carbonate system is adequate though it could with advantage be considered in more detail in relation to the hydrogen-ion concentration. The nitrogen and phosphorus cycles are given the attention their importance requires, though the author is sceptical of the overriding influence that has been ascribed to them by some workers on seasonal variation in plants. It is curious that gaseous nitrogen should be regarded as a substance of little interest, for it is probable that an investigation of the activities of nitrifying and denitrifying bacteria in water would yield interesting results.

The necessary physical and chemical foundations having been laid, the next section proceeds to an account of the ecology of lakes. This portion of the book is full of most interesting facts all properly marshalled so as to give a logical and readable story. Two general chapters are followed by detailed consideration of the animals and plants involved. They are discussed community by community, plankton, nekton, benthos and so on. Although the material used is very largely American the general principles which emerge are of almost universal application, particularly as many of the species present in lakes are widely distributed in the North Temperate region. This section ends with a very useful chapter on productivity and the biological classification of lakes, a subject which is in a

very interesting stage of development. In Part IV two special types of environment are considered, ponds and bog lakes. They are treated briefly, but the relation between them and the larger lakes is well brought out. Finally, there is a short account, some thirty pages long, of running waters. This is the least satisfactory part of the book, partly because the biology of rivers and streams has been very little studied and the information available hardly lends itself to general treatment, and partly also because the important work done in Russia and Germany is barely mentioned.

There is a bibliography of over fifty pages, and most important books and papers on fresh waters published up to 1933 (and a few more recent ones) are included, though it is rather surprising that the papers by Southern and Gardiner on Lough Derg, by Dahl on fish production in Norwegian lakes and by Thienemann on German streams are not mentioned.

F. T. K. PENTELOW.

FISHERY PROBLEMS.

William C. Hodgson. *The natural history of the herring in the southern North Sea.* 120 pp. Edward Arnold, London, 1934. Price 3*s.* 6*d.*

C. F. Hickling. *The hake and the hake fishery.* 142 pp. Edward Arnold, London, 1935. Price 3*s.* 6*d.*

THESE two books embody the material of the Buckland Lectures for 1933 and 1934, and their object is to give a simple account of all that is known about herrings and hake. Since both authors have been engaged in intensive research on their subjects for many years the facts they set down and the conclusions they draw may be regarded as the most complete and up to date surveys of these two important fishery problems.

(1) The rock on which most of this detailed knowledge of herrings is built is the use of scale rings as a means of determining the age of the fish, their growth rates, breeding age and even the nature of their environment. By examining samples of herrings at different times in different places, the proportion of fish of different ages is obtained, and this, with a knowledge of their spawning grounds, ocean currents and many other facts, enables accurate forecasting to be made of the crop of herrings for several years ahead. The fish take varying periods (from 3 to 8 years) to reach maturity in different localities and the reason (unknown) for this would seem to be extremely important as it affects the size and quantity of marketable herrings.

There is much to interest (and mystify) any reader in such points as the apparent 3-year periodicity in the appearance of large groups of 3-year-old herrings, the definite correlation of large catches with the full moon, and the shift of plankton, but perhaps the most important conservation idea is that concerning the use of different meshed nets in trawling. During recent years smaller meshes have been used, with the result that many more small herrings are caught than large ones. This killing off of the herrings before they have a chance to grow into good-sized fish is considered to have seriously depleted the stocks of larger fish which are more useful and valuable. It is suggested that an enlargement of the mesh of trawl nets is advisable in the interests of the herring fishery.

Many of the data which are discussed have already been published in official reports and papers or are promised in future publications. It therefore seems a pity that no bibliography is appended, as it would certainly have enhanced the value of the discussions on many aspects in the life of herrings if one could refer to the original figures.

(2) The hake is a much bigger fish than the herring and takes a lot longer to become a good "marketable" product. It follows that it is even more difficult to get a clear picture of the population changes, movements, mortality, breeding, growth rates, food and so on of this fish than of the herring, and one appreciates the enormous amount of work behind the simply written text of this small book.

An interesting correlation has been obtained between the temperature of the sea and the survival of young hake. In warm years the newly hatched fry survive in greater numbers, showing up in large numbers as "small hake" in the trawls 5 years later. There is also some suggestion in the figures available of this survival being of a periodic nature.

The effect of over-fishing is obviously more pronounced than with the herring because the hake takes 10 or more years to become a good-sized fish. The system of dragging a trawl along the sea bottom, as generally practised, results in indiscriminate catches of large and small hake; consequently the hake stand comparatively little chance of surviving for 10 years. In fact, the catch of the larger hake has declined at the rate of about $7\frac{1}{2}$ per cent. per annum since the war: "the hake cannot grow fast enough to make good the loss due to heavy fishing, so that the rate of replacement is always lagging behind the rate of removal". Herring trawls in at least two of the best hake-fishing areas are a cause of serious losses in hake, because the nets used for herrings catch large quantities of very small (worthless) hake which are thus deprived of the chance of becoming big fish. It was estimated that during the herring season of 1934 alone over a million and a half hake were destroyed in this way. As with the herring, the solution of this problem seems to lie in the careful graduation of mesh sizes in all kinds of nets to catch only what is wanted and allow undersized fish to grow into better ones.

A. D. MIDDLETON.

BIRDS OVER THE ATLANTIC.

V. C. Wynne-Edwards. *On the habits and distribution of birds on the North Atlantic.* 113 pp., maps and 3 plates. Boston, U.S.A., printed for the Boston Society of Natural History.

A YEAR or so ago the Cunard Line printed in Montreal a most excellent folder by Mr V. C. Wynne-Edwards which gave a series of pictures illustrating twenty-two species of birds "which lead their gipsy lives somewhere between Europe and America". This small paper was based on eight trans-Atlantic voyages, and its value to the traveller was so obvious that it inspired a hope of a more detailed account from the same writer.

The present paper is clearly a study of the greatest value, covering as it does an area about which nothing but scattered notes has previously been published. Literature on the subject has been exhaustively examined (the bibliography runs to 10 pages), and the author has combined all these published observations with his own, and shows with a series of maps and census graphs the seasonal distributions of a number of birds.

A useful part of the book and one which will appeal especially to the amateur ornithologist is the field characters, which the author has given in considerable detail for some species only, and which leave no excuse for failure to distinguish between such birds as the two large shearwaters, *Puffinus gravis* and *P. kuhlii*; and it is of interest to learn that this difficulty has led to many errors in earlier records in some of our country faunas, though the two species are distinct enough.

Good too is the description of the flight of Leach's petrel, which alone is enough to distinguish it from the two other species of similar size. For the general public equally good field characters for all species mentioned in the book would have been very useful.

There is a good introduction in which a division is suggested of North Atlantic birds into Inshore, Offshore and Pelagic birds. An excellent point is that a great ocean presents a uniformity of conditions unparalleled elsewhere, and yet the birds which frequent the ocean do not belong to one ecological community.

It is obvious that this book provides a considerable extension of our knowledge of the habits and distribution of species of which comparatively little was previously available; and it is one which should be included in the library of every liner crossing the North Atlantic.

A. W. BOYD.

NOTICES OF PUBLICATIONS ON ANIMAL ECOLOGY

The entomological journals have been abstracted by H. F. Barnes and B. M. Hobby; the others by D. H. S. Davis, Charles Elton and A. D. Middleton.

This series of notices covers most of the significant work dealing with animal ecology published in British journals, large and small. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, University Museum, Oxford.

Copies of these abstracts, cut down to a width suitable for pasting on to five-inch index cards, are issued free with the *Journal*. They can also be obtained separately by non-subscribers, from the Cambridge University Press, Fetter Lane, E.C. 4, or through a bookseller, price 3*s*. 6*d*. per annum post free (about 200 notices, in two sets, May and November).

1. GENERAL PAPERS ON PARTICULAR ANIMALS.

See also **125, 135, 137, 138.**

108. Herford, G. M. (1935). "A key to the members of the family Bruchidae (Col.) of economic importance in Europe." Trans. Soc. British Ent. 2, 1–32.

Includes all species of actual or likely occurrence in Britain: the larvae of these beetles live in the seeds of Leguminous plants and cause much damage to peas, beans, lentils, etc.; because of this habit they are often carried from one country to another in cargoes of seeds. The key is amplified by detailed descriptions and well illustrated. It concludes with a table showing the distribution and host plants of each species.

109. Richards, O. W. (1935). "Notes on the nomenclature of the Aculeate Hymenoptera, with special reference to British genera and species." Trans. Roy. Ent. Soc. Lond. 83, 143–76.

The generic and specific names of bees and wasps have never, as a whole, received a thorough revision according to the International Rules of Nomenclature, nor have old types recently been examined. In doing this it is, therefore, hardly surprising that Dr Richards has had to make a large number of nomenclatorial changes. The type of *Apis mellifera* Linnaeus, 1758, is a male honey bee in the Linnaean collection at Burlington House. The type of *A. mellifica* Linnaeus, 1761, is a worker honey bee in the same collection. Both agree with the usual interpretation of the species, but the earlier name should be used.

110. Kerrich, G. J. (1935). "Notes on Ichneumonidae (Hym.) new to or rare in Britain; with a brief review of British lists published since 1915." Trans. Soc. British Ent. 2, 33–46.

Since the publication of Morley's catalogue of British Ichneumonidae (1915) a large number of species have been discovered new to Britain and have been introduced in local lists. All local lists that have appeared since 1915 are here reviewed as a first step towards collation of our knowledge of the family.

111. Cowley, J. (1935). "The generic names of the British Odonata with a check list of the species." In "The generic names of British insects." Roy. Ent. Soc. Lond. part 3, 43–60.

42 species are recognised. Two subspecies of *Sympetrum striolatum* occur in this country.

112. Radford, C. D. (1934). "Notes on mites of the genus *Myobia*." N. Western Nat. 9, 356–64.

Systematic description of some mites from mice, shrews, bats, and a flying fox.

2. ECOLOGICAL SURVEYS AND HABITAT NOTES.

(*a*) MARINE.

See also **169, 189.**

113. Gardiner, A. P. (1934). "The littoral zone." J. Conch. 20, 65–76.

A useful guide to zonation in the littoral region with notes on the flora and fauna of selected localities.

114. Matthews, L. Harrison (1934). "The sea fish and fisheries of the Bristol district." Proc. Bristol Nat. Soc. 7, 442–62.

A detailed and interesting summary of past and present fishing methods in the Bristol Channel and lower Severn. In this area most of the fishing has always been done by means of fixed nets on the foreshore—a method made successful by the very big tidal range. In recent years competition with the more highly organised deep-sea fisheries has reduced the foreshore ones, except as regards salmon which are still important. Shrimps are also an important item. "The fishermen say that about once every ten years the Severn shrimps appear in enormous numbers." The various methods are of interest: *salmon pools; putchers* (conical basket traps for salmon); *kypes* (conical basket traps for shrimps and small fish); *stow nets* (mainly for sprats); *spillers* (hooks and lines for cod and congers); *swing nets* (buoyed instead of staked—for sprats, etc.); *hose* or *shrimp nets* (rather similar to the last); *apron nets* (not used now—for sprats, whiting and cod); *wall nets* (stretched tight on stakes instead of loose—for rays, flounders, etc.); *trammels* (weighted and floated nets for the same purpose); also *seines, skim nets,* and *Parret salmon nets.* There is a list of sea fish in the area, with notes on those of importance in the fisheries.

115. Moore, H. B. (1932). "Faunistic records for the Manx region." Proc. Liverpool Biol. Soc. 46, 152–9.

Lists of various marine animals, with habitat data for most of the records, for the Isle of Man region.

116. Burton, M. (1932). "The Porifera of the Isle of Man." Proc. Liverpool Biol. Soc. 46, 167–9.

A complete list of species of sponges hitherto recorded from the sea-coasts of the Isle of Man.

(*b*) FRESHWATER.

See also **203.**

117. Leach, A. C. (1934). "The birds of Barrow Gurney reservoirs." Proc. Bristol Nat. Soc. 7, 463–9.

Scattered notes on the occurrence of birds in various years on three reservoirs, with a complete list of species recorded.

118. Britten, H. and **Williams, E. G. (1934).** "Notes on the survey of the natural history of a small area." N. Western Nat. 9, 256–60 and 335–45.

Further notes on a marshy and fresh-water area in Cheshire: vegetation and invertebrates.

119. Pinniger, E. B. (1933). "Notes on the dragonflies of Epping Forest." London Nat. for 1932, 66–72.

A list of species with some ecological notes.

120. Grensted, L. W. (1935). "The Trichoptera of the Oxford district." Trans. Soc. British Ent. 2, 68–72.

47 species are recorded from the Oxford district.

(*c*) LAND.

See also **173, 196, 198.**

121. Flintoff, R. J. (1935). "The weights and measurements of stoats and weasels." N. Western Nat. 10, 29–34.

Stoats: average 11 oz. (male), 8 oz. (female). Weasels: average 3·7 oz. (male), 3 oz. (female).

122. Lockley, R. M. (1935). "The good life on an island: Bardsey." Countryman, 11, 51–69.

A general description of Bardsey Island (North Wales) in winter, with notes on the people, agriculture, and birds. Also a useful map.

123. Lloyd, B. (1934). "Birds of Bardsey Island." N. Western Nat. 9, 331–4.

Lists 44 species seen during a week's visit in June 1933, and gives references to previous records.

124. Knowles, R. E. (1935). "Quail breeding in Merionethshire." British Birds, 28, 315.

Bred in 1933 and probably in 1934 near Lake Bala.

125. Taylor, E. (1935). "Notes on Oniscoidea (woodlice) with a preliminary list of the Oxford species." Proc. Rep. Ashmol. Nat. Hist. Soc. for 1934, 19–22.

14 species are recorded from the Oxford district; useful references to the literature of woodlice are given.

126. Harrison, G. H. (1935). "The natural history of South Rona: Psyllidae." Scottish Nat. 57–60.

Lists, with some ecological notes, of Psyllidae (jumping plant lice) and Odonata (dragonflies) on this island.

127. Stainer, J. (1934). "Handlists of the Plecoptera, Psocoptera, Ephemeroptera, Hemiptera, Neuroptera, Mecoptera, Trichoptera, Ichneumonoidea, Cynipoidea, and Chalcidoidea of the Marlborough District (10 miles radius)." Rep. Marlborough Coll. Nat. Hist. Soc. for 1933, 82, 47–65.

Further notes; also *ibid.* Rep. for 1934, 83, 33–45.

128. Stainer, J. (1935). "A supplement to the handlists of Diptera, Hymenoptera Aculeata, Paraneuroptera (Odonata), and Orthoptera of the Marlborough District (10 miles radius), 1924." Rep. Marlborough Coll. Nat. Hist. Soc. for 1934, 83, 100–105.

129. Thornley, A. (1935). "A provisional list of Cornish insects. Part II." Trans. Soc. British Ent. 2, 87–114.

This part only deals with 3 families of flies and records (with localities) 131 species of Syrphidae, 130 Tachinidae and 180 Muscidae.

130. Audcent, H. (1934). "Bristol insect fauna. Diptera (Part VI)." Proc. Bristol Nat. Soc. 7, 433–41.

Records for a number of families of flies, with a few habitat notes.

131. Thompson, H. W. (1933 and 1934). "Plant pests in Glamorgan." Trans. Cardiff Nat. Soc. 64, 98–101 and 65, 116–20.

List of insects of economic importance and damage done in different places, with dates.

132. Bagnall, R. S. (1931). "Some insects of the buckthorn." London Nat. for 1930, 75–6.

Records from *Rhamnus*: gall midges in the flowers and fruit; leaf galls caused by Psyllids, a mite, and gall midges; and leaf mines caused by three species of moths.

133. Morley, C. (1935). "A beech-tree's insects and their parasites." Ent. Mon. Mag. 71, 90–1.

134. Donisthorpe, H. (1935). "The entomology of a heron's nest." Ent. Rec. 47, 69–71.

Records of Coleoptera, Diptera, Lepidoptera, Hemiptera, Hymenoptera, Collembola, Diplopoda, Pseudoscorpionina, Araneina and Acarina sifted or bred from a nest obtained in Richmond Park, Surrey, in December, 1934.

135. Donisthorpe, H. (1935). "The British fungicolous Coleoptera." Ent. Mon. Mag. 71, 21–31.

A series of lists with annotations.

136. Stainer, J. (1934). "Hymenoptera at Manningford Bruce." Rep. Marlborough Coll. Nat. Hist. Soc. for 1933, 82, 108.

List of 12 species from a mud wall in Wiltshire.

137. Richards, O. W. (1935). "*Bombus muscorum* (Linnaeus) and *B. smithianus* White (Hym.)." Trans. Soc. British Ent. 2, 73–85.

Describes the various subspecies of these two humble-bees and discusses their distribution, pointing out that in the British Isles *B. smithianus* has a fringing distribution (Shetland, Outer Hebrides, Tiree and Coll, Aran Islands, Scilly Isles and Alderney) which closely parallels that of voles.

138. Benson, R. B. (1935). "The high mountain sawflies of Britain (Hymenoptera Symphyta)." Trans. Roy. Ent. Soc. Lond. 83, 23–39.

18 species of sawflies are at present known to inhabit the arctic-alpine botanical regions of the high mountains in the British Isles; 13 of these are new to Britain and 4 new to science, but zoologically and even more especially entomologically the high mountains in Britain are as yet largely unexplored. The Scotch arctic sawfly fauna appears to show several affinities with that of arctic Lapland, though it is not nearly so rich in species. When the mountains of Norway are further explored they will probably be found to possess a fauna linking that of Scotland with that of Lapland.

139. Richards, O. W. (1935). "Some breeding records of Diptera." J. Soc. British Ent. 1, 80–1.

Records insects bred from the nests of the wasps *Vespa rufa* and *Crabro leucostomus*. Also parasites of larvae of the moths *Acronycta aceris* and *Plusia* sp.

140. Barnes, H. F. (1935). "Notes on the Timothy grass flies (*Amaurosoma* spp.)." Ann. Appl. Biol. 22, 259–66.

Two species of *Amaurosoma* were studied: *armillatum* and *flavipes*. Two parasites, *Microbracon exhilarator* and *Lamprotatus* sp., are recorded from Slough. There are indications that a dwarf strain of Timothy grass is less liable to attack; this may be due to the fact that it is an early-flowering strain or that there is varietal resistance.

141. King, L. A. L., Meikle, A. A. and **Broadfoot, A. (1935).** "Observations on the Timothy grass fly (*Amaurosoma armillatum* Zett.)." Ann. Appl. Biol. 22, 267–78.

Two parasites, *Seladerma laetum* and *Dacnusa semirugosa*, are recorded from the West of Scotland. The nature of the attack and the life history and characteristics of the insect in its different stages are described.

142. Barnes, H. F. (1935). "On the gall midges injurious to the cultivation of willows. II. The so-called 'shot hole' gall midges (*Rhabdophaga* spp.)." Ann. Appl. Biol. 22, 86–105.

The biology, host plants and parasites of four species of gall midges are recorded. In three instances the midge is restricted to one species of host plant. All four species reproduce by means of unisexual families.

143. Aubrook, E. W. (1935). "Notes on the biology of *Micromus aphidivorus* Schrank (Planipennia Hemerobiidae)." N. Western Nat. 10, 34–6.

Describes the life history of this lace-wing, which fed on rose aphids in captivity.

3. ANIMAL BEHAVIOUR AND THE ACTION OF ENVIRONMENTAL FACTORS.

See also **176, 181, 183, 190, 200, 210, 220.**

144. Craster, J. M. (1935). "The power of scent." Vasculum, 21, 47–8.

Gives examples of the scenting power of the hare and weasel and its apparent absence in the pheasant.

145. Vanderplank, F. L. (1934). "The effect of infra-red waves on tawny owls (*Strix aluco*)." Proc. Zool. Soc. London, 505–7.

An important experimental study indicating that the eyes of tawny owls are sensitive to infra-red radiation. The pupils of the eyes contracted and the owl was dazzled by an intensity of infra-red light which produced no reaction in the human eye. Living mice, rats, frogs, beetles, etc., were found to give off sufficient infra-red to affect a photographic plate, and presumably for the owl to see them. Dead animals and meat were not seen in the dark by the owl, but when they were so illuminated the owl invariably saw and ate them.

146. Boyd, A. W. (1935). "Notes on the tree sparrow." British Birds, 28, 347–9.

Further notes on the colony described in *British Birds*, 25, 278–85; 26, 273–4; and 27, 256–60. Includes notes on ringing, breeding, enemies (little owls and stoats), and parasites.

147. Burkitt, J. P. (1935). "An attempt to chart fluctuations in the song of the song-thrush, blackbird and chaffinch." British Birds, 28, 364–7.

The dawn chorus begins progressively earlier before sunrise from February to May (increasing from 40 to 84 min.). Similarly the time that it goes on after sunset also lengthens.

148. Ashmore, S. E. (1935). "Time of singing of the goatsucker." British Birds, 28, 259–60.

The incidence of singing after sunset and before sunrise is connected with the intensity of light and is affected by the moon.

149. Clancey, P. A. (1935). "On the habits of kingfishers." British Birds, 28, 295–301.

Comprehensive notes on the activities of three birds on the White Cart River (Renfrewshire) during 1934.

150. Oldham, C. (1935). "Great crested grebes at the Tring Reservoirs." British Birds, 28, 250–6.

On account of the drought no grebes bred here in 1934. They attempted to nest, but were unable to adjust themselves to the abnormal conditions, and they left in midsummer. This departure was not due to food shortage, since there were plenty of fish in the pools that remained: it seems to have been due to the failure to breed.

151. Longwell, J. and **Pentelow, F. T. K.** (**1935**). "The effect of sewage on brown trout (*Salmo trutta* L.)." J. Exp. Biol. 12, 1–12.

The decomposition of sewage uses up a large amount of oxygen. Sewage affects trout not only by lowering the oxygen content of the water, but also by direct toxic effects mainly through sulphides derived from sulphates acted on under anaerobic conditions in mud. These conclusions are supported by a series of observations and experiments. A slow-flowing river may have conditions suitable for production of toxic sulphides without actually having low oxygen content in the water as a whole.

152. Lloyd, Ll. (**1935**). "The bacteria beds of sewage works as an environment for insects." Proc. Roy. Ent. Soc. Lond. 10, 34–9.

The nearest approach to bacteria beds in nature is afforded by a pebble bed, or a moraine, in the spray of a waterfall. There is no important difference in temperature at various depths, and the mean monthly temperatures are more equable and higher than the shade temperatures for the district. This tends to give the insect denizens a different season and in some cases a more protracted season than the like species breeding naturally. Another segregating factor is given by the vast area and the depth of the habitable zone in the beds compared with the shallow zones available to the same species in nature. There is some slight zoning of the larvae in the bed, but one can say that the breeding ground is almost as the cube compared to the square of a natural habitat. Therefore, successful insects breeding in the beds emerge in numbers so vast that inbreeding must be the rule. At Leeds over 200,000 insects have been surveyed and about 80 species recognised, but of these 30 occurred only once, and only 2–5 individuals were taken of 20 other species. Any or all of these 50 may be stragglers on the beds. Three species are generally abundant (a Chironomid and 2 Psychodid flies). A predacious Cordylurid fly is also general and seasonally abundant, but not in comparable numbers.

153. Marshall, J. (**1935**). "The location of olfactory receptors in insects: a review of experimental evidence." Trans. Roy. Ent. Soc. Lond. 83, 49–72.

An excellent examination of present knowledge of this subject. The literature of the olfactory sense is reviewed with especial reference to the limits of the sense and the location of the organs concerned. The various views about the chemical senses in insects are given. Recent work supports the view that the olfactory organs are located on the antennae, although the possibility that the olfactory organs may also act as receptors of contact chemical stimuli is suggested.

154. Myers, J. G. (**1935**). "Experiments with spiders and the bee-like *Eristalis tenax* Linn." Proc. Roy. Ent. Soc. Lond. 9, 93–5.

It would appear that the treatment meted out to a victim depends very little on its size and vigour (save in extreme cases like the bumble-bee), but almost entirely on its species, though the idiosyncrasy of the individual spider is a factor. *Eristalis tenax* (the drone fly) was treated like a bee and not like a fly of the same bulk.

155. Gunton, H. C. (**1935**). "Phenological records." Proc. Roy. Ent. Soc. Lond. 10, 11.

If we wish to be able to gauge the prospects of emergence in any ordinary, or extraordinary, season containing the fluctuations of temperature which are so usual, it appears that we must disregard to a large extent the average or accumulated temperatures of the season and concentrate on the close observance of the alternating warm and cold spells in relation to the normal dates of emergence which are being approached, bearing in mind the portion of the average weekly temperature curve which has been reached and the characteristics of the different species.

156. Tulloch, J. B. G. (**1935**). "*Vanessa atalanta*, *Scoliopteryx libatrix* and *Triphosa dubitata* hibernating in caves." Entomologist, 68, 93–4.

A definite record of one red admiral butterfly hibernating (January 1934) in a limestone cave at 1200 ft. up on Mynydd Llangattwg, a mountain north of Brynmawr. Dozens of herald moths and hundreds of tissue moths were also found.

157. Tulloch, J. B. G. (1935). "Where do 'Red Admirals' go to in the winter in England?" Entomologist, 68, 31–3.

Contains observations that this butterfly goes up into the branches of an old cedar tree each night in Monmouth in the autumn. Further references in **F. W. Frohawk**, *ibid.* 99; **F. D. Welch**, *ibid.* 114–15; **C. Nicholson**, *ibid.* 115.

158. Adkin, R. (1935). "*Laspeyresia* (*Carpocapsa*) *pomonella* L.: some notes on its life history in Britain." Entomologist, 68, 25–6.

The earliest date of emergence of this moth is June 16th (1933) and the latest July 30th (1930), the chief emergence taking place during the last week in June and the first fortnight in July. By this time the apples are well formed. The writer dispels the long-cherished idea that the moths of the first flight invariably lay their eggs in the eyes of the apple. He finds the eggs are deposited anywhere on the fruit, occasionally on the stalk and rarely on the leaves. The larvae enter the fruit at the eye but more often at some part of the side of the apple.

159. Gunn, D. L. (1935). "The temperature and humidity relations of the cockroach. III. A comparison of temperature preference, and rates of desiccation and respiration of *Periplaneta americana*, *Blatta orientalis* and *Blatella germanica*." J. Exp. Biol. 12, 185–90.

Two species choose temperatures at which they are not liable to suffer from drying up. The rate of drying up is higher in smaller species with larger surface-volume ratio. It also depends on the thickness of the integument. One species (*B. germanica*) will enter high temperatures which would be fatal in the absence of water to drink: it usually occurs, however, within reach of water; also its reaction to temperature changes after it has begun to dry up.

160. Varley, G. C. (1935). "A new Syrphid larva and some other aquatic insect larvae which obtain their oxygen from plant roots." Proc. Roy. Ent. Soc. Lond. 10, 30–1.

The larva of the Syrphid fly, *Chrysogaster hirtella*, the puparium of the Ephydrid fly, *Notiphila riparia*, and the larva of the Chrysomelid beetle, *Donacia semicuprea*, were found living in mud in the river Cam, and they constitute a very remarkable case of convergence in their special respiratory adaptations. Each pierces the roots of the grass *Glyceria aquatica*, by means of the spine-like hind-spiracles, and so obtains a supply of oxygen from the intercellular spaces of the plant.

161. Nixon, G. E. J. (1935). "Notes on wasps. IV." Ent. Mon. Mag. 71, 106–11.

Describes how in an experiment a *Vespa germanica* queen will accept a *V. vulgaris* nest and, provided that the *vulgaris* workers will tolerate her, how she will behave exactly as if she were among workers of her own kind and allow them to bring up her progeny. A wild thriving nest of *vulgaris* has been found with a *germanica* queen.

162. Davies, W. M. and **Hobson, R. P. (1935).** "Sheep blowfly investigations. I. The relationship of humidity to blowfly attack." Ann. Appl. Biol. 22, 279–93.

The eggs and young larvae of *Lucilia sericata* are extremely sensitive to desiccation at 37° C. The micro-climate at the base of the wool is normally too dry for the development of maggots except in the region of the rump, which often is moist owing to soiling with faeces and urine. The humidity at the base of the wool appears to be the main factor which determines susceptibility of the sheep to attack.

163. Hobson, R. P. (1935). "Sheep blowfly investigations. II. Substances which induce *Lucilia sericata* Mg. to oviposit on sheep." Ann. Appl. Biol. 22, 294–300.

Various putrefying substances induce oviposition on sheep in the field; excreta of *Lucilia* larvae, faeces from scouring sheep, stale urine and bacterial cultures are effective. But the flies do not oviposit on these substances unless they are placed close to the skin of a live sheep. The natural odour of the sheep may be responsible.

164. Evans, A. C. (1935). "Studies on the influence of the environment on the sheep blow-fly, *Lucilia sericata* Meig. II. The influence of humidity and temperature on prepupae and pupae." Parasitology, 27, 291–8. "III. The influence of humidity and temperature on the adult." Parasitology, 27, 299–307.

The life conditions were determined experimentally in terms of temperature and humidity. The effects of different diets on the adult were also studied, in relation to viability, weight, and reproduction.

165. Howes, N. H. and **Wells, G. P. (1934).** "The water relations of snails and slugs. I. Weight rhythms in *Helix pomatia* L." J. Exp. Biol. 11, 328–43. "II. Weight rhythms in *Arion ater* L. and *Limax flavus* L." *Ibid.* 11, 344–51.

The weights of all three species show remarkable fluctuations, due to variation in water content, which tend towards periodicity at intervals of several days. These rhythms in water content are partly independent of environmental conditions; it seems likely that aestivation may occur either as a result of external dry conditions or of the fact that a snail is at the bottom of its hydration cycle.

166. Fox, H. Munro, Simmonds, B. G. and **Washbourn, R. (1935).** "Metabolic rates of Ephemerid nymphs from swiftly flowing and from still water." J. Exp. Biol. 12, 179–84.

The metabolic rate (oxygen consumption) is correlated with the swiftness of the water in which the mayfly nymphs live. There is also some correlation between the habitat and the resistance to relative oxygen deficiency.

167. Fox, H. Munro (1935). "The vapour pressures of the blood of arthropods from swift and still fresh waters." J. Exp. Biol. 12, 174–8.

It was known that certain arthropods (caddis and mayfly larvae, and *Asellus*) had a higher oxygen consumption in swift-flowing water than in still water. Experiments showed that the osmotic pressure of the blood had no relation to such differences of oxygen consumption.

168. Van Dam, L. (1935). "A method for determining the amount of oxygen dissolved in 1 c.c. of water." J. Exp. Biol. 12, 80–5.

This method for measuring the amount of oxygen in very small quantities of water has the added advantage of enabling very low oxygen contents to be analysed.

169. Orton, J. H. (1932). "Studies on the relation between organism and environment." Proc. Liverpool Biol. Soc. 46, 1–16.

Mainly a summary of various observations by the author on the ecology of marine molluscs such as limpets and oysters, illustrating the nature of their physiological and ecological adaptations.

170. Orton, J. H. (1935). "Biology of growth and breeding." Nature, 135, 509.

Oysters go on growing longest in water whose summer temperature rises slowly, since breeding begins (and growth ceases) at 15–16° C. A similar phenomenon is found in *Zostera marina*.

171. Beadle, L. C. (1934). "Osmotic regulation in *Gunda ulvae*." J. Exp. Biol. 11, 382–96.

An analysis of changes that take place when this flatworm is put in sea water of varying dilutions and composition.

4. PARASITES.

See also **133, 139, 146, 200.**

172. Radford, C. D. (1935). "Mites found upon the white rat." N. Western Nat. 10, 42.

Myobia ensifera and *Notoedres muris* found on both wild brown and tame albino rats: the *Notoedres* caused severe scabs, mainly on the ears. *Laelaps echidninus* on the brown rat only.

173. Thompson, G. B. (1935). "The parasites of British birds and mammals. III. On some parasites living in the nest of the house martin (*Chelidon u. urbica* Linn.)." Ent. Mon. Mag. 71, 46–50.

174. Thompson, G. B. (1935). "The parasites of British birds and mammals. IV. Records of bat parasites." Ent. Mon. Mag. 71, 143–7.

175. Marples, G. (1935). "Parasite on robin and great tit." British Birds, 28, 311.

Ornithomyia avicularia, a parasitic fly, was found commonly on the robin and once on other birds examined (a great tit).

176. Salt, G. (1935). "Experimental studies in insect parasitism. III. Host selection." Proc. Roy. Soc. B, 117, 413–35.

Experiments with the Chalcid *Trichogramma evanescens* showed that ovipositing females choose hosts by size only, having a preference for objects (even seeds and grains of sand or globules of mercury) which are larger than themselves. Strains reared exclusively on the eggs of the small moths *Sitotroga* and *Ephestia* for many generations showed no preference for their normal host, but invariably accepted the largest object (within limits) for oviposition. It is suggested that choice of host by size alone must seriously affect the population increase of the parasite, since females must waste time and eggs on useless things such as sand, seeds, or eggs of species which are physiologically unsuitable for the parasite.

5. FOOD AND FOOD-HABITS.

See also **131, 132, 143.**

177. Drummond, J. C. and **MacWalter, R. J. (1935).** "Pro-vitamin A in the food of whales." J. Exp. Biol. 12, 105–7.

Whales have a large amount of vitamin A in their livers. Analysis of whale food samples (mainly Euphausids) showed that a pigment similar to astacin (allied to but not the same as carotene) was present, and that this is probably converted by whales into vitamin A. Since feeding tests to rats show that zooplankton in general is a poor source of vitamin A, it is concluded that certain fish and whales may manufacture it from this pigment as well as accumulating it from 300 plankton.

178. Gray, R. W. (1935). "Diet of seals." Nature, 135, 473.

Seals examined by various people contained fish, cuttlefish, squids, Crustacea, and Mollusca. The need for a proper investigation of the food of seals, in relation to the fisheries, is pointed out. **F. Greenshields** (*ibid.* 657) found 4 seals from the River Tay to have stomachs full of fish (flatfish, sprats, and some salmon smolts), also Crustacea, mainly fish parasites.

179. Nicholson, C. (1935). "Moths eaten by bats." Entomologist, 68, 61.

A list of 11 species.

180. Dallman, A. A. (1934). "Greenfinches and Mezereon." N. Western Nat. 9, 277–8.

Eating the seeds of *Daphne mezereon*.

181. Collenette, C. L. (1935). "Notes concerning attacks by British birds on butterflies." Proc. Zool. Soc. London, Part 2, 202–17.

A number of observations of birds attacking butterflies, with species and localities. There is a chart showing the types of beak marks made by different birds on butterflies' wings.

182. Hicks, J. B. (1933). "Butterflies and birds." London Nat. for 1932, 114.

Old and young house martins eating the butterflies *Aphantopus hyperanthus* and *Epinephele janira* in North Devon in July. They ate the wings as well as the bodies.

183. Caton Haigh, G. H. (1935). "On pink-footed geese." British Birds, 28, 368–70.

Barley oat and wheat stubbles are favourite feeding grounds in autumn. The geese also eat young self-sown corn, rye grass and small potatoes. In winter they frequent grass fields. They have never been known to eat clover. The weight of the geese varies from 4 to 8 lb., the majority being between 6 and 7 lb.

184. Brown, R. H. (1935). "The food of certain birds of prey." British Birds, 28, 257–8.

List of birds and mammals found near the nesting places of tawny owl, barn owl, peregrine falcon, merlin, kestrel, common buzzard, and sparrowhawk, in Westmorland in 1934. Also the stomach contents of a heron from Cumberland.

185. Parsons, B. T. (1935). "Food of kestrel." British Birds, 29, 28.

At a nest near Cissbury, Sussex: 12 voles, 6 house-mice, 7 shrews, 3 young starlings, 1 young lapwing, 1 house-sparrow, 1 linnet, 1 chaffinch, and 1 hedge-sparrow.

186. Moxon, P. (1934). "Sparrow-hawk and jay." Rep. Marlborough Coll. Nat. Hist. Soc. for 1933, 82, 105.

Sparrow-hawk killing a jay.

187. Hibbert-Ware, A. (1935). "The little owl: an examination of its food habits." School Nature Study, 30, 45–7.

Feeds on mice, voles, rats, shrews, beetles, insect larvae, and earthworms. There is no evidence of it taking game or poultry. These conclusions are supported by analysis of some thousands of pellets, of food stores and 7 gizzards, and observations.

188. Pearce, E. J. (1935). "Water-beetles as food for fish." Ent. Mon. Mag. 71, 18.

The beetle contents of the stomach of a grayling (*Thymallus vulgaris*).

189. Raitt, D. S. (1935). "The occurrence of four species of sand eels, of economic importance, in Scottish waters, one of which is new to science." Scottish Nat. 61–2.

Ammodytes marinus, a new species, is apparently abundant, and, together with the other three, forms an important fish food.

190. Pethen, R. W. (1934). "Some observations on the glowworm, *Lampyris noctiluca* L." London Nat. for 1933, 38–44.

Includes a number of original observations by the author, on life history, habits etc. In several experiments the beetles while emitting their light were eaten by toads.

191. Spittle, R. J. (1933). "A feeding habit of *Ophonus rufibarbis* F. (Col.)." London Nat. for 1932, 92.

Carabid beetle eating ripening fruits of *Pastinaca sativa*.

192. Spittle, R. J. (1933). "A feeding habit of *Vespa vulgaris* Linn." London Nat. for 1932, 114.

Wasps gnawing off flowerheads of thistles (*Carduus arvensis*) and sucking the plant juice.

193. Norris, M. J. (Mrs O. W. Richards) (1935). "A feeding experiment on the adults of *Pieris rapae* L. (Lepid. Rhop.)" Entomologist, 68, 125–7.

That butterflies do require a sugar diet and not merely water as has been shown previously (Proc. Zool. Soc. Lond. 1934, 333–60) to be the case with moths of the genus *Ephestia*.

194. Hamilton, M. A. (1935). "Further experiments on the artificial feeding of *Myzus persicae* (Sulz.)." Ann. Appl. Biol. 22, 243–58.

Myzus persicae were fed on media of which one constituent was a radioactive indicator containing polonium. The aphides picked up the indicator from the medium and transmitted it to the leaves on which they were subsequently fed. A constant proportion of the amount imbibed was transferred to the leaves, therefore it was deduced that the polonium was transmitted through the bodies of the aphides and not on the outsides of the stylets.

195. Herford, G. V. B. (1935). "Studies on the secretion of diastase and invertase by *Empoasca solana* Delong (Rhynchota, Homoptera, Jassidae)." Ann. Appl. Biol. 22, 301–6.

The diastase, besides being secreted in the salivary glands, is apparently also formed by certain yeasts which are regurgitated from the gut. A technique is described for feeding the leaf-hoppers on a liquid. An enzyme (probably invertase) which inverts pure sucrose is also secreted.

196. Goddard, W. H. (1935). "A record of the Hemiptera Heteroptera at the Imperial College Field Station, Slough, Bucks, with notes on their food." Trans. Soc. British Ent. 2, 47–67.

Many Heteropterous bugs commonly considered to be phytophagous also show carnivorous habits. Of 70 species collected, 34 were observed to feed on aphides, but of these only 4 were definitely carnivorous. 2 species would feed on plants, but preferred aphides, while one species fed on aphides, but preferred plants. 27 species showed that some specimens will feed on aphides, but further experiments are necessary to show which foods they prefer; of these, however, 4 showed no preference for either aphides or plants. 6 species were definitely vegetarians.

6. ANIMAL POPULATIONS.

See also **113, 123, 224.**

197. Rogers Brambell, F. W. (1935). "Reproduction in the common shrew, *Sorex araneus* L." Philos. Trans. Roy. Soc. London, B, 225, 1–62.

1064 shrews were caught, mostly in the Bangor district, and examined. Details are given of the state of the reproductive organs throughout the year. Shrews remain sexually immature until April or May of the year following their birth, and die by the end of their first breeding season, which lasts from about May to September or October.

198. Hardy, E. (1935). "Bird concentration in a small area in Lancashire." British Birds, 29, 25–6.

In one of several hour counts there were 359 birds of 29 species on a sewage farm near Liverpool.

199. Marples, G. (1935). "Some results of trapping and ringing." British Birds, 29, 22–5.

Gives the live weights of a number of birds. A trap census of tits in a garden over 3 hours was done. About five times as many birds were caught in 3 hours as were ever seen at one time in the garden.

200. Boyd, A. W. (1935). "Report on the Swallow Enquiry, 1934. Publication of the British Trust for Ornithology." British Birds, 29, 3–21.

This enquiry was started with the object primarily of establishing the average size of broods of the swallow in relation to the time of year and environment, and secondarily of taking a census of breeding birds in different areas. The results of reports from 22 observers (12 of whom carried out censuses) are analysed in full. The relation of swallows to other birds such as house-martins, occurrence of parasites, and other ecological matters are also discussed.

201. Wontner-Smith, C. (1935). "Number of young reared by the rook." British Birds, 29, 26–7.

The average brood of young rooks reared near Leeds in 1933–5 was 1·97.

202. Burkitt, J. P. (1935). "Notes on the rook: with special reference to the proportion of young in flocks and the change over from the winter roost to the rookery." British Birds, 28, 322–6.

In north-west Ireland in winter young rooks tend to group themselves and do not visit the rookeries after the autumn.

203. Serle, W. and Bryson, D. (1935). "Distribution and number of the dipper on the N. and S. Esks (Midlothian)." British Birds, 28, 327–31.

A census of the winter and summer populations on these two rivers and their tributaries was made between November 1933 and June 1934. The winter territory is more extensive than the summer one because of the poorer feeding conditions in winter, and the greater number of birds. In winter there were 190 dippers on 65 miles of rivers—roughly 1 bird to a third of a mile; in summer 54 pairs on 40 miles, or 2 birds to a mile and a half.

204. Ticehurst, N. F. (1935). "Former abundance of black grouse in Sussex." British Birds, 29, 31.

Black grouse (*Lyrurus britannicus*) lived in Ashdown Forest about a hundred years ago.

205. Rowberry, E. C. (1934). "Gulls in the London area." London Nat. for 1933, 48–58.

During the last 50 years gulls have become increasingly numerous in the London area. This paper summarises the literature on the subject since 1850 and the author's own observations. "From 1900 until the present time our gull population has assumed immense proportions." The black-headed gull first appeared up the Thames in numbers during severe winters in 1887–8, 1892–3, and 1894–5, invading also the parks. By about 1926 they had become established as inland visitors in London. Part of the increase was probably due to foreign immigrants (as suggested by ringing records): at any rate it appears to be due to over-population of the coast areas. Similar notes are given for other species, and about roosting, flight-lines, etc. Gulls probably consume enormous quantities of earthworms on grassland.

206. Lloyd, B. (1935). "The great crested grebe at Elstree Reservoir." British Birds, 29, 28–9.

Elstree Reservoir is 20 miles south-east of Tring. Two or three pairs usually breed there. In 1934 they tried to breed but failed.

207. Hollom, P. A. D. (1933). "The great-crested grebe in the London area." London Nat. for 1932, 51–6.

Results of census enquiries for the area within 20 miles' radius of the centre of London, with notes on the seasonal occurrence and numbers of grebes on reservoirs.

208. Nicholson, E. M. (1935). "An index of heron population." British Birds, 28, 332–41.

Following the heron census of 1928 the British Trust for Ornithology has arranged an annual sample census to keep track of annual fluctuations. Taking the 1928 figure as 100, the 1934 sample gave a figure of 102. This sample represents about a quarter of the entire heron population of England and Wales, and is based on counts for the whole of the Thames basin plus selected points throughout the country.

209. Glegg, W. E. (1935). "The history of Essex heronries." Essex Nat. 24, 254–65.

210. Miles, H. W. (1935). "Biological studies of certain species of *Caliroa* Costa and *Endelomyia* Ashmead (Hymenoptera Symphyta)." Ann. Appl. Biol. 22, 116–33.

Growth rates of the larvae are included and reproduction is mainly dependent on parthenogenesis.

211. Tulloch, J. B. G. (1935). "Longevity of *Nymphalis io*." Entomologist, 68, 16.

The life span of the peacock butterfly is stated to be from 9 to 10 months.

212. Poulton, E. B. (1935). "Assemblages of Coccinellid beetles; also of the Danaid butterfly *Danaus plexippus* Linn., during hibernation or migration." Proc. Roy. Ent. Soc. Lond. 9, 108–9.

In these assemblages various possible interpretations are to be borne in mind: (1) *Migration*, ensuring that the bands are not scattered and dissipated; also that both sexes are represented. (2) *Hibernation*, ensuring these same conditions during and at the end of the winter sleep. (3) *Promotion of cross-breeding*, due to the assemblage at one spot of insects scattered over a wide area. (4) *Enhancement of aposematic effect*, apparently nearly always present.

213. Hobby, B. M. and **Elton, C. (1935).** "Mortality in the dung-fly, *Scatophaga stercoraria* Linn. (Dipt., Cordyluridae)." J. Soc. British Ent. 1, 71–2.

Mortality, apparently caused by the parasitic fungus *Empusa muscae*, was widespread in this one species of dung-fly in 1933, and in two places at least (Kidlington, Oxon, and Pevensey, Sussex) it was unusually severe in that year.

214. Gause, G. F. (1935). "Experimental demonstration of Volterra's periodic oscillations in the numbers of animals." J. Exp. Biol. 12, 44–8.

In a very simple "community" consisting of one species of prey and one species of predator periodic oscillations would, according to Volterra's theory, occur in the two populations. Gause had already shown that with two species of Protozoa (predator and prey) under laboratory conditions both species died out after the first "cycle"; although if immigration was permitted at a certain rate, oscillations occurred. The present experiments (with yeast as prey and *Paramecium* as predator) were done under carefully controlled conditions which resulted in a periodic oscillation: plotted as the number of predators against the number of prey, the curve continues to go round in a circle. The possible reasons why the predator does not completely wipe out the yeast are not discussed.

7. MIGRATION, DISPERSAL, AND INTRODUCTIONS.

See also **117, 123, 150, 156, 157, 200, 205, 206, 207, 212.**

215. Witherby, H. F. (1935). "The 'British Birds Marking Scheme'. Progress for 1934." British Birds, 28, 302–8.

There was a large increase in the amount of ringing done in 1934.

216. Kenrick, W. E. (1935). "A greenfinch 'homing' experiment." British Birds, 28, 276–7.

Birds returned to the trap after being released from 2 to 10 miles away in all directions, in urban and country areas near Birmingham.

217. Smith, W. C. (1932). "The Manx herring shoals during the seasons of 1929, 1930 and 1931." Proc. Liverpool Biol. Soc. 46, 108–38.

A statistical study of sizes, breeding condition, and food of herrings round the Isle of Man, and of the inshore and offshore movements during the fishing season (June to September). The old and young herrings have different times and degree of movement which are discussed.

218. Daniel, R. J. and **Fleming, R. A. (1933).** "Plaice-marking experiments in the Irish Sea, 1929–31." Proc. Liverpool Biol. Soc. 47, 17–70.

Notes on further recoveries of some of the thousand marked fish released between Liverpool and Anglesey. Nearly all the fish moved southwards and were found as far away as the Bristol Channel and south-east Ireland. There is a good map showing the results of the movements.

219. Nicol, J. M. (1935). "A note on the ant *Camponotus* (*Tanaemyrmex*) *maculatus* F. in gum acacia." Ent. Mon. Mag. 71, 67.

Wooden cases of this gum export from West Africa were found to be swarming with this ant on arrival at a London wharf.

220. Davies, W. M. (1935). "Studies on aphides infesting the potato crop. III. Effect of variation in relative humidity on the flight of *Myzus persicae* Sulz." Ann. Appl. Biol. 22, 106–15.

Controlled laboratory experiments demonstrated an inhibitive action of high humidities upon flight. It is suggested that this influence of humidity upon flight is the explanation of the fact that in North Wales infestations of aphides are always greater following a period of east winds.

221. Fox-Wilson, G. (1935). "*Phylloxera* on vines, a new British record." Proc. Roy. Ent. Soc. Lond. 10, 25–8.

The vine Phylloxera (*Daktulosphaira vitifoliae*) was recognised in this country in Berkshire in 1934. A map is given showing its occurrence since the first records from Hammersmith in 1863.

222. Adkin, R. (1935). "*Gracillaria azalella*, Brants, at Eastbourne." Entomologist, 68, 17.

The spread of this *Azalea* pest is noted. In 1925 (**1926**, *ibid.*, 59, 13) it was reported from greenhouses at Torquay; later (**1930**, Ent. Rec. 42, 45) from a greenhouse at Salisbury, and now as captured in a light trap at Eastbourne.

223. Cockayne, E. A. (1935). "*Sidemia zollikoferi* (Freyer)." Entomologist, 68, 73–6.

A Noctuid moth probably immigrant from Russia. Includes data on the 5 specimens caught in this country previous to 1934 and also the 7 specimens captured in 1934.

224. Dannreuther, T. (1935). "Migration records." Entomologist, 68, 5–9.

A general summary for 1934 together with comparative estimates of abundance in 1934. Further references in **T. Greer**, *ibid.* 92; **T. Dannreuther**, *ibid.* 111, 136 and 139–41; **H. G. Harris**, *ibid.* 136.

225. Riley, N. D. (1935). "Records of *Polygonia c-album* in 1934." Entomologist, 68, 69–71.

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CHARLES ELTON

and

A. D. MIDDLETON

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